UNGULATE RESPONSES TO MULTI-USE PATHWAY CONSTRUCTION AND USE IN GRAND TETON NATIONAL PARK, WYOMING

FINAL REPORT
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ABSTRACT

In 2006 Grand Teton National Park (GTNP) adopted a transportation plan which includes the construction of paved, multi-use pathways along existing park roads to accommodate non-motorized travelers, raising concerns about potential impacts of the pathway on wildlife and wildlife viewing experiences. We initiated a repeated measures Before-After-Control-Impact (BACI) study to assess the potential effects of pathway construction and use on the distribution and behavior of ungulates (elk, pronghorn antelope, moose, mule deer) and on wildlife viewing opportunities. Data collection occurred before pathway construction (2007), during construction (2008) and for two years after the pathway was open to public use (2009 and 2010) in a 6.9 km control region (without pathway) and a 12.5 km treatment region (with pathway) along Teton Park Road. If ungulates responded to pathway construction and use, we predicted that, in the treatment as compared to the control: 1) standardized counts of ungulates viewed from the road would decline; 2) ungulates would be detected farther from the road; and 3) the probability of ungulates responding behaviorally would be higher. Further, if ungulates avoided pathway activities, we expected wildlife viewing activities to decrease in the treatment compared to the control after pathway installation. During 20 months of data collection over the four years of the study, we conducted 421 road surveys, collecting observations during 5,126 sampling miles driven, recording 23,424 human activities and 2,319 ungulate groups comprised of 14,769 observations of individual ungulates; additionally, we conducted 670 focal samples recording 151 hours of ungulate behaviors. Park visitors stopped and were seen afoot and on bicycles in the treatment more often than in the control. When the pathway opened in 2009, bicyclists switched from using the road to using the path, and there was an overall increase in bicycling and pedestrian activities on the pathway in 2009 and 2010. More people were observed viewing wildlife in the treatment compared to the control throughout the study. Notably, we saw a three-fold increase in off-road human activity in the treatment after the pathway was constructed, an activity with a greater potential to disturb wildlife than activities that remain on the road and pathway. We observed elk most frequently, followed by pronghorn, while we observed moose and mule deer relatively infrequently. Moose and mule deer were observed in the treatment more frequently than the control, and did not seem to be displaced by pathway activities, although observations were limited. During early season (June-July 15), the number of elk viewed in the treatment was stable or increased slightly, while elk viewed in the control

decreased between 2008 to 2010. In mid season (July 16-August 31), when park visitation and pathway use peaked annually, elk appeared to less be behaviorally responsive in the treatment compared to the control after pathway installation. These results are contrary to predictions that elk would avoid pathway activities and suggest that elk might have developed tolerance to human activities in the treatment. During mid season, pronghorn were seen, on average, about 164 meters farther from the road in the treatment in 2010 compared to 2007, but shifted closer to the road in the control area over the same period. This suggests that pronghorn did to a limited degree avoid habitats proximate to the road where the pathway was installed, supporting one of our predictions indicative of a pathway effect. Overall, while pathway construction and use resulted in direct habitat loss and widened and diversified the human footprint, our results did not consistently demonstrate alterations in ungulate distribution and behavior or wildlife viewing opportunities, with the exception of a relatively modest shift in pronghorn distribution, and an apparent decrease in the behavioral responsiveness of elk, during periods of peak visitation and pathway use.

INTRODUCTION

Transportation systems in national parks allow millions of people to see and experience an array of natural and cultural resources that park managers aim to protect in perpetuity. Roads and automobile traffic in parks and elsewhere impose negative impacts on natural terrestrial and aquatic systems, destroying and altering habitats, spreading non-native biota (Trombulak and Frissell 2000), modifying and creating barriers to animal movements (Riley et al. 2006), masking and interfering with animal auditory communications and sensing (Barber et al. 2010), and killing organisms that attempt to cross roads but are struck by vehicles (Trombulak and Frissell 2000, Evink 2002, Forman 2003). Road impacts on wildlife are considered a concern for park managers (Ament et al. 2008). To reduce motor vehicle impacts on park resources, diversify recreational experiences, and increase safety for non-motorized travelers, there is a growing interest in alternative transportation options such as recreational pathways to complement park roads.

While the inclusion of pathway systems accommodates non-motorized travel for park visitors, with the potential to reduce traffic congestion and decrease bicycle-automobile conflicts, such infrastructure widens travel corridors and extends the influence of humans into habitats that may be important to wildlife. Human disturbance has been shown to affect different ecological characteristics of wildlife, such as home range size and habitat use, foraging behavior, reproductive success, body condition, disease susceptibility, sex ratio, daily activity period, social development, mating systems and social structure (see review in Bejder et al. 2009). In parks where wildlife are seen near roads, recreational activities on pathways may prompt local wildlife to change activity patterns, avoid habitats near recreational pathways, and increase vigilance and energy expenditures (Knight and Cole 1995, Borkowski et al. 2006, George and Crooks 2006). Adding a recreational pathway along a well-traveled road known for wildlife viewing opportunities is unprecedented in a US national park (National Park Service 2006), thus it is uncertain how this new infrastructure might affect wildlife and wildlife viewing opportunities and experiences.

In 2006 Grand Teton National Park (GTNP) adopted a Transportation Plan that calls for a paved, multi-use pathway system to accommodate bicyclists, pedestrians and other non-motorized travel modes (National Park Service 2006). Under the plan, approximately 30.3 km (18.8 miles) of existing roadways could be reconstructed and widened to include multi-use pathways, while another 36.0 km (22.5 miles) of paved pathways could be installed 15.2 to 45.7 m (50 to 150 feet) from existing roads that traverse open habitats occupied by large ungulates (pronghorn antelope [*Antilocapra americana*], elk [*Cervus elaphus*], moose [*Alces alces*], and mule deer [*Odocoileus hemoinus*]) which may be seen from park roads during summer and fall months. This pathway would widen and diversify the "human footprint", extending visitor activities further into wildlife habitats and raising concern about how this new infrastructure may affect behaviors, movements and interactions of animals and park visitors coinciding in these park travel corridors. Park management contracted several independent studies to quantify and assess effects of the first phase of pathway construction (12.5 km, 7.7 miles, constructed in 2008) and use on birds, bears and ungulates, including this study, which focuses on ungulates, park visitors and their interactions in the pathway corridor.

The goal of this field research was to assess if and how pathway construction and use affects distribution and behavior of pronghorn, elk, moose and mule deer, as well as visitors' wildlife viewing opportunities and interactions with wildlife in GTNP. To accomplish this goal, we implemented a repeated measure environmental impact Before-After-Control-Impact (BACI) study design (Stewart-Oaten et al. 1986, Green 1993, Stewart-Oaten and Bence 2001, Smith 2002, Roedenbeck et al. 2007). Data collection occurred before pathway construction (2007), during construction (2008) and for two years after the pathway was open to public use (2009 and 2010) in a control region (without pathway) and a treatment region (where the pathway was constructed). We sampled human activities along with the number of ungulates observed in the control and treatment areas, how close ungulate groups were to the transportation corridor and the behaviors of ungulates to understand if they were affected by pathway activities. If ungulates avoided pathway construction and use, we predicted that during and after pathway construction, compared to the control: 1) standardized counts of ungulates observed in the treatment would decline, 2) ungulates would be detected farther from the transportation corridor in the treatment, and 3) ungulates would exhibit increased behavioral responsiveness in the treatment area. We also expected to see changes in the types and frequencies of human activities occurring in the treatment area with the installation of the pathway. If wildlife were negatively affected by these changes and avoided habitats near the road and pathway, we would expect to see fewer people watching wildlife in the treatment area after the pathway was constructed and opened.

STUDY AREA

This study was conducted in Grand Teton National Park (GTNP) in northwestern Wyoming, USA (43-50'00" N, 110-42'03" W). The study area included habitats visible from the 19.4 km (12 miles) of the Teton Park Road (TPR) between Moose and Spalding Bay Road, at the southern and northern extents of the study area, respectively (Figure 1). This section of the TPR traversed the valley floor between the Teton Mountains to the west and the Snake River to the east; study area landscapes visible from the TPR spanned elevations from 2133 meters (6998 feet) at the northern end of the study area to 1962 meters (6437 feet) at the southern end of the study area. The landscape visible from the TPR was characterized by flat, open, glacial outwash valley plains with vegetation dominated by dry sagebrush (*Artemesia* spp.) shrublands with patches of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menzesii*), Engelman spruce (*Picea engelmannii*) and smaller stands of aspen (*Populus tremuloides*) woodlands providing cover for wildlife. Willow (*Salix* spp.) riparian zones and cottonwoods (*Populus angustifolia*) lined the streams, ponds and remnant irrigation water features in the study area.

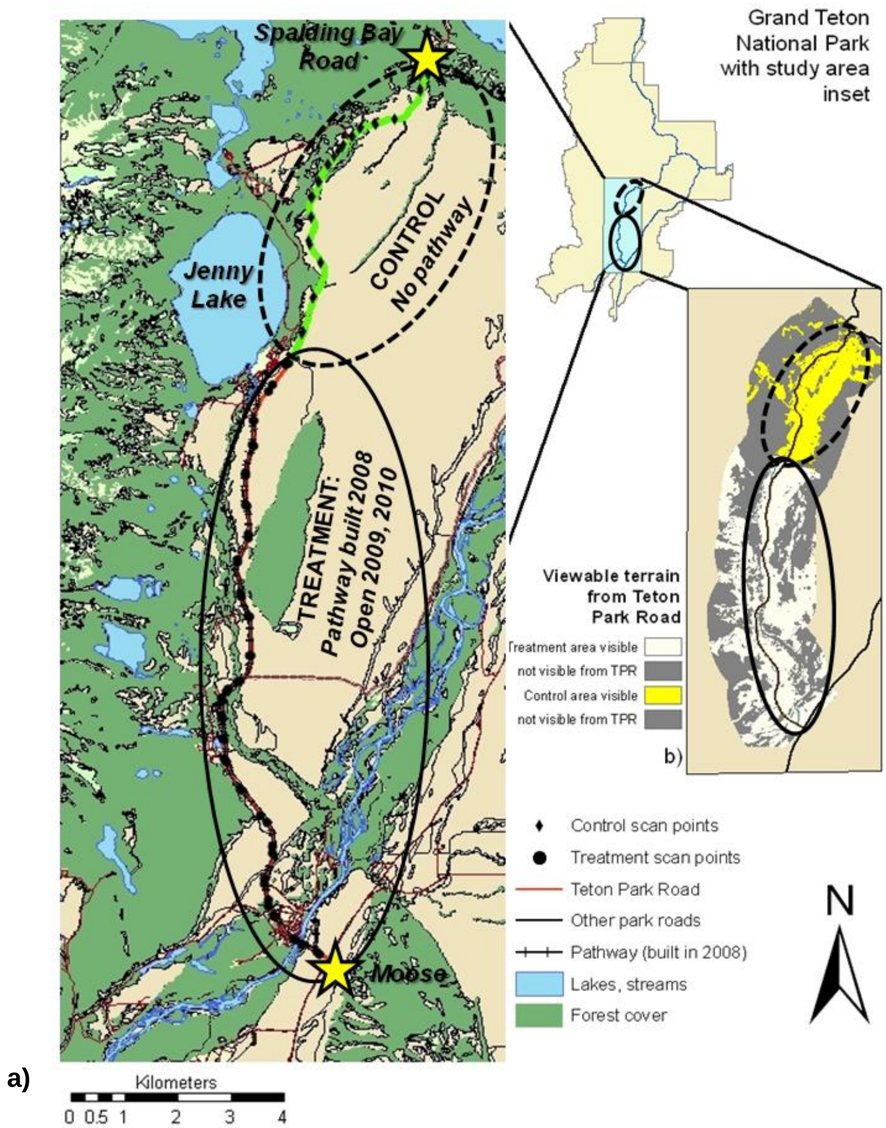

Figure 1. The study region included habitats visible from 19.4 km (12 miles) of the existing Teton Park Road (TPR) between Moose and Spalding Bay Road (marked with stars, inset a). Viewshed analysis estimated area visible from 42 established scan points along the TPR in both areas (control scan points =17; treatment scan points = 25; inset b). In 2008, construction of 12.5 kilometers (7.7 miles) of paved pathway next to the road created a "treatment area" (solid ellipses) while the northern 6.9 km (4.3 miles) of the TPR in the study region had no pathway and served as a "control area" (dashed ellipses).

The study area provided summer and fall habitat for resident and migrating ungulates, including elk, pronghorn antelope, mule deer, and moose. Grizzly and black bear (*Ursus arctos horribilus* and *Ursus americanus*), grey wolves (*Canis lupus*), mountain lions (*Felis concolor*), coyotes

(*Canis latrans*) and red fox (*Vulpes vulpes*) have been known to use study area habitats as well. Additionally, thousands of park visitors pass through the study region on the TPR each year, with a peak in visitation typically occurring in July. While most people travel through the study area on the TPR in an automobile, a small portion of visitors opted for non-motorized travel modes and recreation (e.g., bicycling, walking).

In 2008, 12.5 kilometers (7.7 miles) of pathway was constructed along the TPR in the southern end of the study area to accommodate non-motorized travel between South Jenny Lake and Moose. The installation and public use of the 3.05 meter (10 foot) wide paved route along the existing road created a “treatment” region within the larger study area (Figure 1). The northern end of the study area, along 6.9 km (4.3 miles) of the TPR between South Jenny Lake Junction and Spalding Bay Road, provided a “control” site where no pathways were constructed during this study. Although the control and treatment areas similarly shared the same habitats and types of topographical features, the two adjacent areas were not identical in size or configuration. These distinctions were considered in our analyses and interpretation of results.

METHODS

We applied a repeated measures Before-After-Control-Impact (BACI) approach to assess the potential effects of pathway construction and use on ungulates (Stewart-Oaten et al. 1986, Green 1993, Stewart-Oaten and Bence 2001, Smith 2002, Roedenbeck et al. 2007). We conducted systematic road surveys and focal sampling methods to repeatedly measure variables of interest in the treatment and control area before (2007), during (2008) and after (2009-2010) the pathway installation and use in the treatment region. Our assessment focused on four response variables: 1) numbers of ungulates viewed (standardized by viewable area) per survey; 2) distance of ungulate groups to TPR; 3) probability of ungulates behaviorally responding during a group behavior scan; and 4) probability of ungulates behaviorally responding during focal animal sampling. We also sampled human activities occurring in the study area during road surveys as an index of potential change in stimuli which might be related to ungulate responses. If trends in the response variables were similar in the control and treatment area over the years (before, during and after pathway introduction), it would imply that the pathway, introduced into the treatment area in 2008, did not influence the response variables. Alternatively, if trends in response variables were different in the treatment and control area after pathway installation, this would then suggest that ungulates may have responded to pathway activities.

Field methods

Road survey methods involved two observers systematically traversing the 19.4 km (12 mile) TPR study area, from Moose to Spalding Bay Road (or vice versa; survey direction was alternated), to sample human and ungulate activities which could be observed from the road. Surveys were conducted typically 1-2 times a day from June through October, with start times staggered 12-14 hours (e.g., Day 1: 6am & 6pm; Day 2: 8am, 8pm, etc.). Surveys typically spanned 2-4 hours depending on ungulate activity in the corridor. Some surveys spanned both light and dark periods (as defined by sunset/sunrise tables); however, most surveys were initiated and completed during daylight conditions.

Observers traveled in a truck at ~48 km/h (~30 mph) through the study area, stopping at 42 “scan points” established approximately ~160-804 meters (~0.1-0.5 miles) apart in select locations where views of the landscape were maximized (Figure 1). Observers also stopped opportunistically to record data (described below) if ungulates were observed between scan points. At each scan point, immediately upon stopping, and prior to our presence and activities potentially influencing visitor behavior, observers sampled human activities occurring within 200 m of the scan point. This included recording the number of autos stopped on the side of the road (i.e., gravel shoulder) and in paved pullouts, the number of pedestrians (i.e., people afoot) and bicyclists on the side of the road and in paved pullouts, and the number of pedestrians and bicyclists on the pathway in the treatment in 2009 and 2010. Non-motorized activities were further distinguished by movement (passing versus stopped) when first observed. In 2008, 2009, and 2010, we recorded whether people were viewing wildlife and all human activities off-road and off-pathway. If ungulates were visible when the observers first stopped at a scan point, observers would note the majority of the group’s behavior and approximate location when first seen, in case the group disappeared while human activities were being recorded.

After recording human activities, observers searched the landscape for ungulates using binoculars. An ungulate group was defined as ≥1 ungulate(s), with nearest neighbor distances between ungulates <100 meters (328 ft) within groups and >100 meters between groups. When ungulate groups were observed at any point during road surveys (i.e., at and between scan points), observers recorded the time of observation, species, location, and the total number of animals in the group. Location of the group was determined based on the observers' location, distance between observers and the ungulate group, and a compass azimuth to the center of the group. Distance from observers to the group was determined using a laser range finder; if the group was beyond the effective range of the laser range finder, we used the azimuth to the group and a topographic map to estimate a distance from observer to group. If the group was observed within ~500 meters of the TPR, one observer scanned and recorded each animal's behavior in the group. These behaviors were categorized in a manner similar to definitions by Childress and Lung (2003) and Borkowski et al. (2006), as follows: bedded; feeding; grooming (i.e., licking or scratching oneself or another); scanning (i.e., standing with head at or above shoulder level, but not apparently alarmed); traveling (i.e., walking); vigilant (i.e., displaying alarm or acute attention toward some stimulus); flight (i.e., running away from some stimulus); defensive (i.e., kicking, biting or charging towards another animal); and mating (i.e., rut behaviors observed in the fall months such as grouping and pursuing cows or sparring between bulls).

In addition to recording scan behaviors of each ungulate in a group, we conducted focal animal samples, collecting continuous behavioral observations of individual animals both during road surveys and opportunistically (e.g., prior to and after surveys); we avoided collecting >1 focal sample from the same group in a day, as possible. We adapted focal animal sampling methods from Childress and Lung (2003) When an ungulate group was sighted within 500 meters of the road, we collected the same attributing data as described in road survey methods. One observer randomly selected an individual from the group and continuously recorded behaviors categorized as described above for approximately 15 minutes during road surveys. If the focal animal sample occurred opportunistically before or after a road survey, observers continued focal sampling as long as possible or until the focal animal moved out of sight.

Data Analysis

We calculated annual means and standard errors (SEs) of human activities observed within 200 meters of scan points in the treatment and control by summing each category of activities seen in each area per survey and dividing that value by 25 or 17 scan points in the treatment or control area, respectively. Wildlife viewing activity was reported as present or absent at each scan point; annual summaries of this activity are reported as the mean percent of scan points where wildlife viewing was occurring per survey, by area (i.e., treatment and control).

Individual road surveys conducted during daylight and crepuscular periods served as the experimental unit to analyze numbers of ungulates viewed. To standardize number of ungulates viewed in the treatment and control given that these areas were not identical in size or configuration, we divided the count of ungulates viewed, per survey, by hectares (ha) of habitat that could be seen from the road in each area. The area of habitat visible from the road was estimated using a viewshed analysis in a Geographic Information System (GIS; ArcMap v9.3, ESRI, Redlands, CA); see inset b in Figure 1 for representation of viewshed output. The estimation of hectares of visible terrain accounted for differences in the control and treatment regions, and for different heights (hence, different detectability) of large (moose, elk) and small (mule deer, pronghorn) ungulates. In the control area, elk and moose counts for each survey were divided by 986 ha (3.81 square miles) of visible terrain, whereas deer and pronghorn counts were divided by 932 ha (3.60 square miles). In the treatment area, elk and moose counts per survey were divided by 2,261 ha (8.73 square miles) and pronghorn and deer counts were divided by 2,111 ha (8.15 square miles). We refer to this standardized measure (views per viewable area) as "animals viewed", and graphically display mean numbers and standard errors of animals viewed per survey for effects plots.

We used observations of ungulate groups during daylight and crepuscular conditions as the experimental unit to analyze distances of ungulates to the TPR. We used a GIS to determine perpendicular distance (meters) of each group to the TPR based on the group's location. Means and standard errors of perpendicular distances were presented in effects plots. Distance values to the TPR exceeding 1000m were difficult to accurately estimate. Thus, for statistical analyses, values exceeding 1000m were reclassified to equal 1000m to reduce variability in the data while retaining observations of groups that could be seen at extremely far distances from some points on the TPR.

For group scan and focal animal sampling behavioral analyses, we created a binomial response variable, pooling flight, vigilance, traveling and defensive behaviors as “responsive” behaviors, and bedded, feeding, grooming, scanning and mating behaviors as “non-responsive” behaviors (Goldstein 2005). For group scan data, this binomial response variable estimated the probability that an individual within a herd was responsive. For focal animal data, this binomial response variable measured the probability that the focal animal was responding each second during the focal sampling period. For scan samples, we created effects plots of the annual mean (and SE) proportion of animals responding per group (number responsive / total number animals in group). Similarly, for focal animal samples, we plotted the mean (and SE) proportion of time an individual was responding per focal sample (number of seconds responsive / total seconds in the focal sample).

We modeled the effect of year (2007, 2008, 2009, 2010), area (treatment, control) and time (day, crepuscular) on each response variable (ungulates viewed per survey, distance from road per group, probability of an individual during group behavior scan, and probability of an individual responding during focal sample). Time was defined as “day” if the sample occurred entirely during daylight conditions (≥1 hour after dawn and ≥1 hour before dusk), or as “crepuscular” if any portion of the survey or observation was recorded during crepuscular hours (≤1 hour after dawn or ≤1 hour prior to dusk) as determined by regional sunrise and sunset tables (U.S. Naval Observatory 2010).

We square root-transformed the two continuous response variables (animals viewed per survey, distance from road per group) to meet the assumption of linearity and used a linear mixed model to evaluate whether fixed effects and their interactions influenced numbers of ungulates viewed and ungulate distances to the TPR, as follows:

$$X_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \tau_{l(i)} + (\alpha\beta)_{ij} + (\alpha\gamma)_{ik} + (\beta\gamma)_{jk} + (\alpha\beta\gamma)_{ijk} + \varepsilon_{ijkl}$$

where μ is the overall mean, α_i is the fixed effect of year (i = 2007, 2008, 2009, 2010), β_j is the fixed effect of area (j = control(0), treatment(1)), γ_k is the fixed effect of time (k=day(0), crepuscular(1)), $(\alpha\beta)_{ij}$ is the interaction between year and area, $\tau_{k(i)}$ is the random effect of survey where $k(i)$ = 1, …, n surveys conducted in year i, $(\alpha\gamma)_{ik}$ is the interaction between year and time, $(\beta\gamma)_{jk}$ is the interaction between area and time, $(\alpha\beta\gamma)_{ijk}$ is the three-way interaction between the three fixed effects, and ε_{ijkl} is the error in the mean not explained by fixed effects. The random effect of survey nested within year was included given that numbers of animals viewed and their location relative to the road in the control and treatment areas during a given survey may be influenced by environmental (e.g., weather, visibility, length and time of day) and biological (e.g., inter- and intraspecific interactions, plant phenology) factors occurring during the survey.

For the binomial response variables, we used logistic regression with a logit link function to assess whether year, area and time and their interactions predicted the probability of an individual responding. For the group scan data, we again included a random effect for survey nested within year; additionally, we included group nested within survey and year to account for potential pseudoreplication issues of correlated behavioral responses within a group, given that an individual's response may be influenced by other group members' behaviors. For the focal animal data, we included a unique integer accounting for the random effect of the date nested within year (as opposed to survey within year), given that focal samples were recorded both during surveys and opportunistically before and after road surveys. This random effect accounted for similar environmental factors (e.g., weather) and biological factors (e.g., presence of other ungulates, predators, humans) shared on days when >1 focal sample was collected.

Each species was analyzed separately. When low sample sizes and high variability prevented statistical modeling of a given response variable (e.g., in the moose and mule deer data), we limited reported results to qualitative assessments of annual means (and standard errors), pooled over seasons and time of day, and limited the interpretations of these results accordingly. We conducted analyses of elk and pronghorn data over three seasons: early season (June to July 15, when ungulates were calving/fawning), mid season (July 16 to August 31, when human visitation and temperatures peaked), and late season (September 1 to October 15, when ungulates were influenced by the rut, hunting pressure beyond the study area and oncoming winter weather conditions).

Statistically significant (p<0.05) interactions indicated a trend observed in a given response variable varied depending on differences in the two or three variables in the interaction. We were particularly interested in significant year*area interactions as an indicator of different responses observed in the treatment area as compared to the control area after pathway activities were introduced. Thus, we ran additional post hoc Tukey-Kramer Honestly Significant Difference (HSD) tests, comparing significant seasonal year*area interactions within each area between years (2007-2008, 2007-2009, 2007-2010, 2008-2009, 2009-2010). We conducted additional post hoc ANOVA analyses to further examine significant seasonal 3-way interactions (year*area*time), excluding the main effect of time from the model and reanalyzing crepuscular and day observations separately, to assess whether the year*area interaction was significant during either time period. We used average values to further interpret significant contrasts between years within an area and to interpret how divergent trends between the treatment and control areas might be indicative of a pathway effect. Results reported in the main text focused on statistically significant main effects and on the interactions incorporating year and area (year*area and year*area*time). Tables with all parameter estimates and p-values for main and post hoc analyses are referenced as well. We used PROC GLIMMIX in SAS (v9.2) for ANOVA analyses and for calculating means and SEs for plotting, and created effects plots using R (version 2.13.1) and Microsoft Office Excel 2007.

RESULTS

We began collecting field data on June 24th in 2007, and on June 5th, 9th, and 10th in the 2008, 2009 and 2010 field seasons, respectively. Our last day of data collection ranged between October 13-16th over the four years of the study. During these four years, we conducted 421 road surveys (Table 1), systematically collecting observations of ungulate and human activities over 5,126 miles driven across the study region. Most road surveys (n = 242 surveys, 57%) were conducted completely during the day while a smaller proportion of road surveys (43%, n = 179 surveys) started or ended during crepuscular periods (Table 1).

Table 1. Road survey effort summarized by year and time of day. Surveys were conducted in Grand Teton National Park between June-October of 2007-2010.

YEAR	TOTAL # surveys	Crepuscular surveys	Day surveys
2007	69	25	44
2008	95	45	50
2009	133	59	74
2010	124	50	74
2007-2010	421	179	242

Human Activities

We sampled human activities observed within 200 meters of 17 scan points in the control on 7,276 occasions and 25 scan points in the treatment on 10,700 occasions, producing 21,483 observations of human activities. A disproportionate number of human activities (84%, n= 18,148 observations) were recorded during day surveys (57% of all surveys), while only 16% (n=3,335 observations) of human activities were sampled during crepuscular surveys. Over the four years of the study, there appeared to be a slight upward trend in the numbers of automobiles observed stopped in the study area during surveys. Most stopped automobiles were seen in pullouts in the treatment area, increasing from an average of 25 to an average of 30 seen per road survey over the four years of the study (Figure 2). In comparison, we saw an average of 2-3 autos in pullouts in the control area per survey. Mean number of automobiles observed stopped along the road per survey in the control was relatively low, from <1 to 2, compared to a 3-5 automobiles seen stopped along the road in the treatment during surveys.

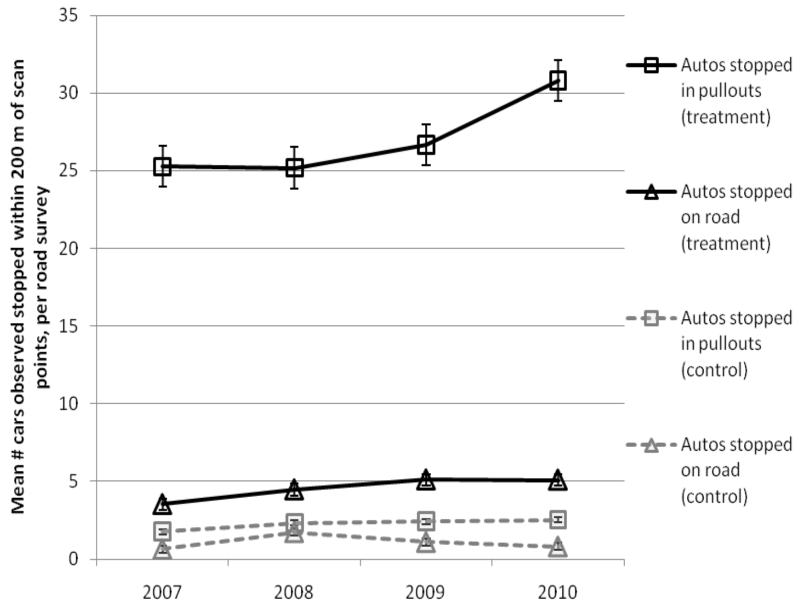

Figure 2. Mean number (± standard error) of automobiles stopped within 200 meters of road survey scan points in the control (n = 17 scan points) and treatment (n=25 scan points) areas during road surveys conducted in Grand Teton National Park between June-October 2007-2011.

Most pedestrian activity was observed in treatment area pullouts (Figure 3). In the control, we saw few pedestrians in pullouts (ca. 2) and afoot on the road (<1) on average, per survey. In the treatment, the mean number of people observed afoot on the road decreased from 6 to 3 people between 2007 and 2010. It was rare to see people off road in the control region, but we saw an increase in people off road and off path in the treatment from about 1 to 3 people per survey between 2008 and 2010 (Figure 3).

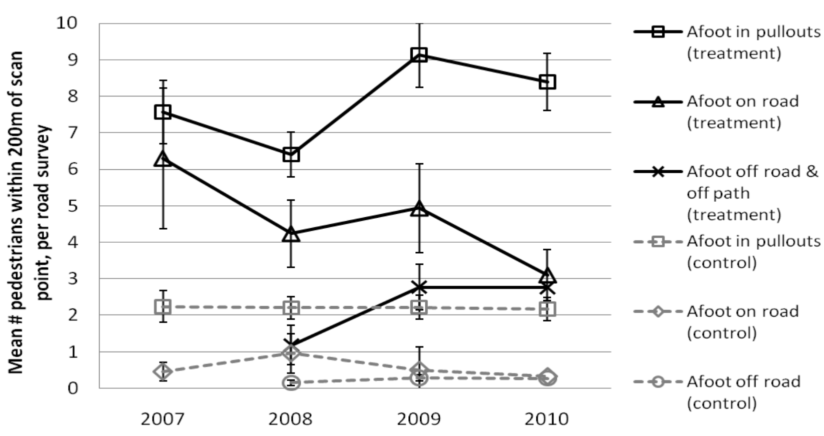

Figure 3. Mean number (± standard error) of people afoot within 200 meters of road survey scan points in the control (n = 17 scan points) and treatment (n=25 scan points) areas during road surveys conducted in Grand Teton National Park between June-October 2007-2010.

On average we saw < 1 cyclist passing on the road in the control per survey, peaking in 2008 (Figure 4). In the treatment, from 2007 to 2008, we observed an increase from 1 to 2 bicyclists passing on the road on average per survey, then decreasing to <1 per survey in 2009 and 2010 coinciding with the opening of the pathway. With the opening of the pathway to public use, we saw 8-9 bicyclists passing on the pathway per survey in 2009 and ca. 7 in 2010 (Figure 5), and recorded 1-2 bicyclists and 2-3 pedestrians stopped on the pathway during each survey.

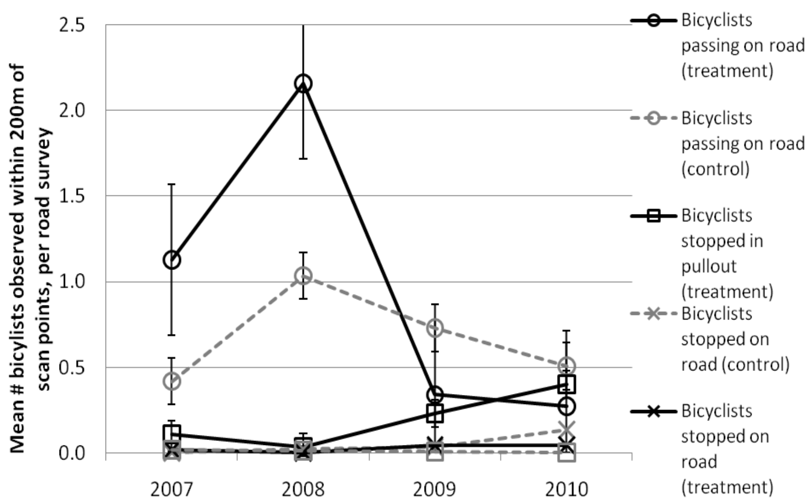

Figure 4. Mean number (± standard error) of bicylists on Teton Park Road within 200 meters of road survey scan points in the control (n = 17scan points) and treatment (n=25 scan points) areas during road surveys conducted in Grand Teton National Park between June-October 2007-2010.

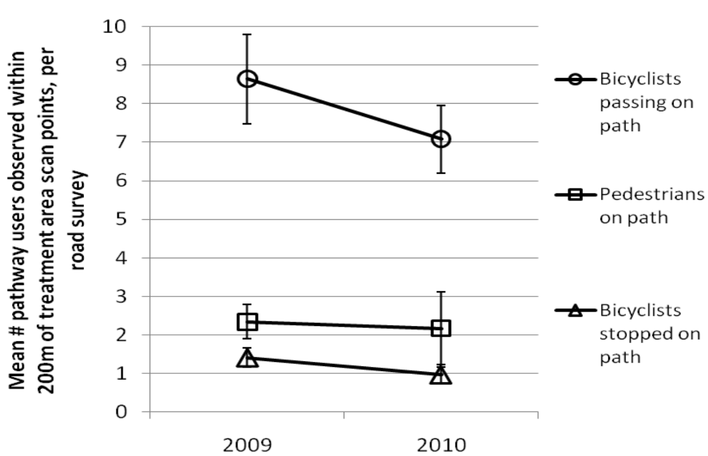

Figure 5. Mean number (± standard error) of pathway users observed within 200 meters of treatment scan points (n=25) during road surveys conducted in Grand Teton National Park between June-October 2009 and 2010.

We recorded at least one person watching wildlife, on average, at about 34% of the 17 control scan points per survey in 2008, but wildlife viewing in the control decreased to ca. 5% and 3.5% in 2009 and 2010, respectively (Figure 6). In the treatment, at least one person per survey was observed viewing wildlife from the road at about 56% of the 25 treatment scan points in 2008, decreasing to about 26% in 2009, and rebounding to 50% in 2010. People were seen watching wildlife from the pathway as well; in 2008, prior to the completion of the pathway, we observed people watching wildlife from the pathway at ca. 3% of the treatment scan points, and this activity increased to ca. 7% and 12% in 2009 and 2010, respectively, after the pathway opened for public use.

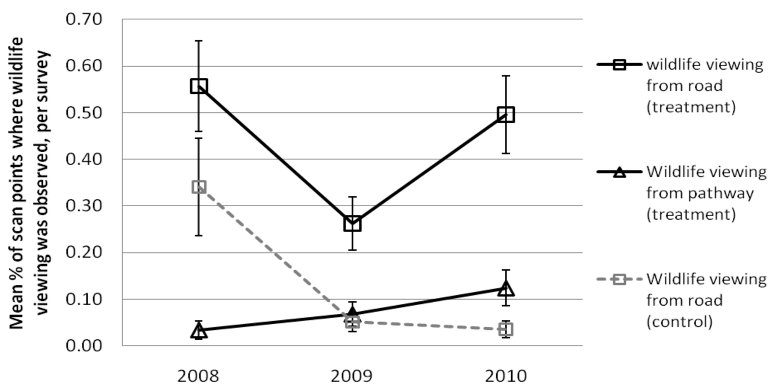

Figure 6. Mean percentage (± standard error) of road survey scan points in the control (n = 17 scan points) and treatment (n=25 scan points) where at least one person was seen viewing wildlife during road surveys conducted in Grand Teton National Park between June-October in 2008-2010.

Ungulate activities

During 421 road surveys, we recorded data on 2,319 ungulate groups, yielding 14,769 individual ungulate observations, with 63% (n= 9,249) observed during day and 37% (n=5,520) during crepuscular surveys. Elk were most commonly observed, comprising 57% of group observations (1,304 elk groups) and 83% of all ungulate observations (12,134 elk observations). Pronghorn comprised 32% of groups observed (728 pronghorn groups) and 14% of all ungulate observations (2,039 pronghorn observations). Mule deer and moose observations comprised only 6% (138 mule deer groups) and 5% (126 moose groups) of group observations, and 2% (257 mule deer observed) and 1% (201 moose observed) of all ungulate observations. We recorded 151 hours of ungulate behaviors over 670 focal animal samples collected in day (n=413 or 56% of focal samples) and crepuscular (n=319 or 43% of focal samples) periods before, during and after road surveys.

Mule Deer – We recorded 257 mule deer observations within 138 mule deer groups (Table 2; Appendix Map 1) during 104 road surveys (25% of 421 survey conducted). Group sizes ranged from 1-9 individuals (mean±SE=1.86±0.12). Only 9% of all mule deer observed (19 groups containing 24 mule deer) were recorded in the control area while most mule deer (233 individuals in 121 groups) were seen in the treatment area (Table 2).

Table 2. Summary of mule deer groups and number within groups observed at crepuscular and day periods in the control and treatment areas during 421 road surveys conducted in Grand Teton National Park between June-October 2007-2010.

	MULE DEER									
	CONTROL AREA				*TREATMENT AREA*					
YEAR	Crepuscular		Day		Crepuscular		Day		*TOTAL GROUPS*	*TOTAL # SEEN*
	groups	# seen	groups	# seen	groups	# seen	groups	# seen		
2007	1	1	4	5	5	12	12	45	22	63
2008	1	3	4	8	8	18	17	28	30	57
2009	0	0	3	3	13	25	21	38	37	66
2010	1	1	3	3	11	18	34	49	49	71
2007-2010	3	5	14	19	37	73	84	160	138	257

Mule deer were seen more often per survey in the treatment in 2007, prior to pathway construction, compared to other years (Figure 7, panel A). The oscillating trend in mule deer group distance from the road in the control (Figure 7, panel B) is based on 19 group sightings over the four years of the study, with annual means that ranged from ca. 84 meters to the TPR in 2009 (n=3) to 239 in 2008 (n=5). In the treatment, annual mean distance to the road ranged from ca. 148 meters in 2008 (n=25) to 222 in 2009 (n=34). Data on behavioral responses in mule deer were scarce and highly variable (Figure 7, panels C & D). The mean proportion of individuals responding in the control was based on only 3, 1, and 3 group observations in 2007, 2008 and 2009, respectively; in 2010, we recorded no mule deer responding in 21 group behavior scan observations in the treatment (Figure 7, panel C). Likewise, in the control, we were able to obtain only 4 focal samples during the four years of the study, totaling only 51 minutes of observation time. In the treatment, based on 8 hours of observations collected during 35 focal samples, the proportion of time spent responding by mule deer in the treatment ranged from approximately 16% to 32%, peaking in 2010 after the lowest level of observed responsiveness in 2008 (Figure 7, panel D).

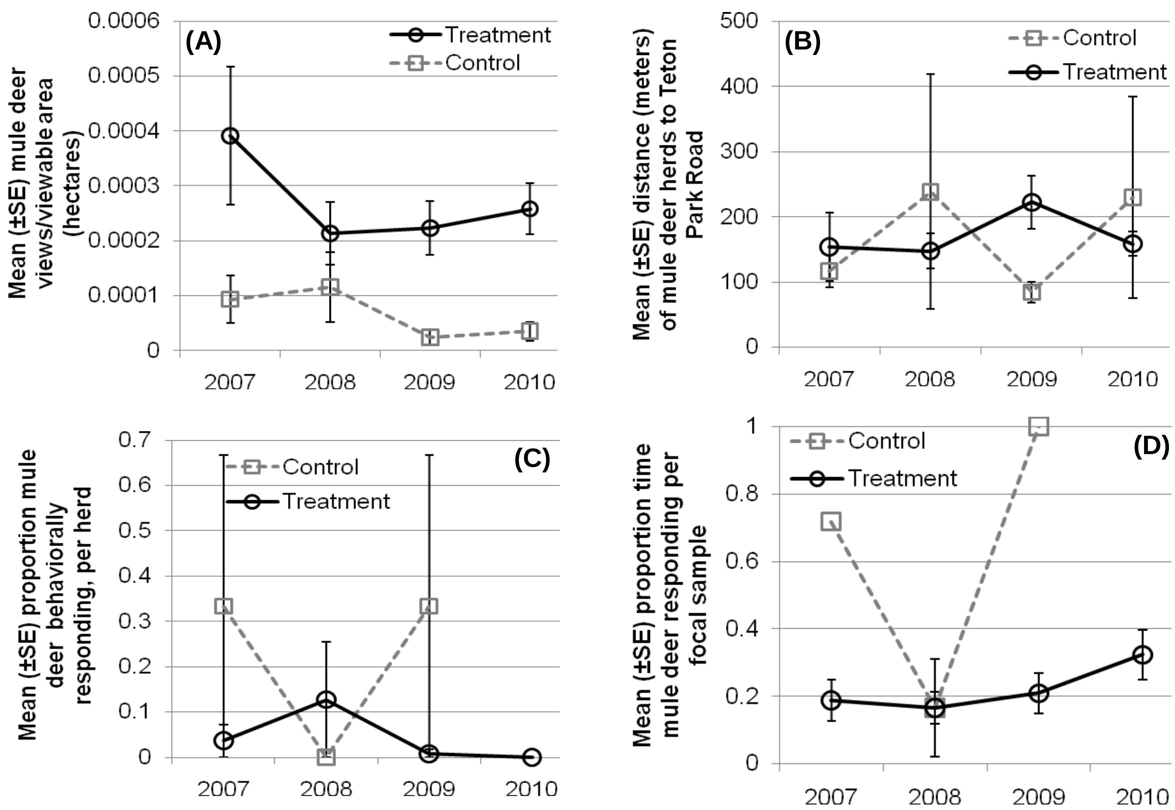

Figure 7. Annual mean (± standard error) A) number mule deer viewed (standardized by viewable area) per survey, B) distance of mule deer from road per group, C) proportion of mule deer responding per group, and D) proportion time of mule deer responding per focal sample in the control and treatment areas in Grand Teton National Park from June-October of 2007-2010.

<u>Moose</u> –Moose observations were also sparse. All but three moose groups observed were seen in the treatment; in 2010, no moose were seen in the control during road surveys (Table 3; Appendix Map 2). Moose group sizes ranged from 1 to 5 individuals (mean±SE=1.59±0.06). Numbers of moose viewed per survey in the treatment appear stable in the first three years and increased in 2010 (Figure 8, panel A). Moose were farther from the road in the treatment in 2008 (337±95.7m) compared to 2007 (145±53.8m), 2009 (186±33.6m) and 2010 (151±15.7m; Figure 8, panel B). Behavioral responsiveness was highly variable in the treatment in 2007 (n=11) and 2009 (n=29); of 8 and 38 group behavior scan in 2008 and 2010, respectively, no moose were responsive in the treatment (Figure 8, panel C). In the control, the 3 groups seen in

the first three years of the study moved out of view before we were able to conduct a behavior scan. The proportion of time moose were observed responding during 46 focal samples totaling over 9 hours of behavioral observations in the treatment ranged between approximately 12% in 2007 and 22% in 2010 (Figure 8, panel D).

Table 3. Summary of moose groups and number within groups observed at crepuscular and day periods in the control and treatment areas during 421 road surveys conducted in Grand Teton National Park between June-October 2007-2010.

	MOOSE									
YEAR	*CONTROL AREA*				*TREATMENT AREA*				*TOTAL GROUPS*	*TOTAL # SEEN*
	Crepuscular		Day		Crepuscular		Day			
	groups	# seen	groups	# seen	groups	# seen	groups	# seen		
2007	0	0	1	1	3	5	10	17	14	23
2008	0	0	1	2	8	12	12	20	21	34
2009	0	0	1	1	15	23	24	37	40	61
2010	0	0	0	0	15	27	36	56	51	83
2007-2010	0	0	3	4	41	67	82	130	126	201

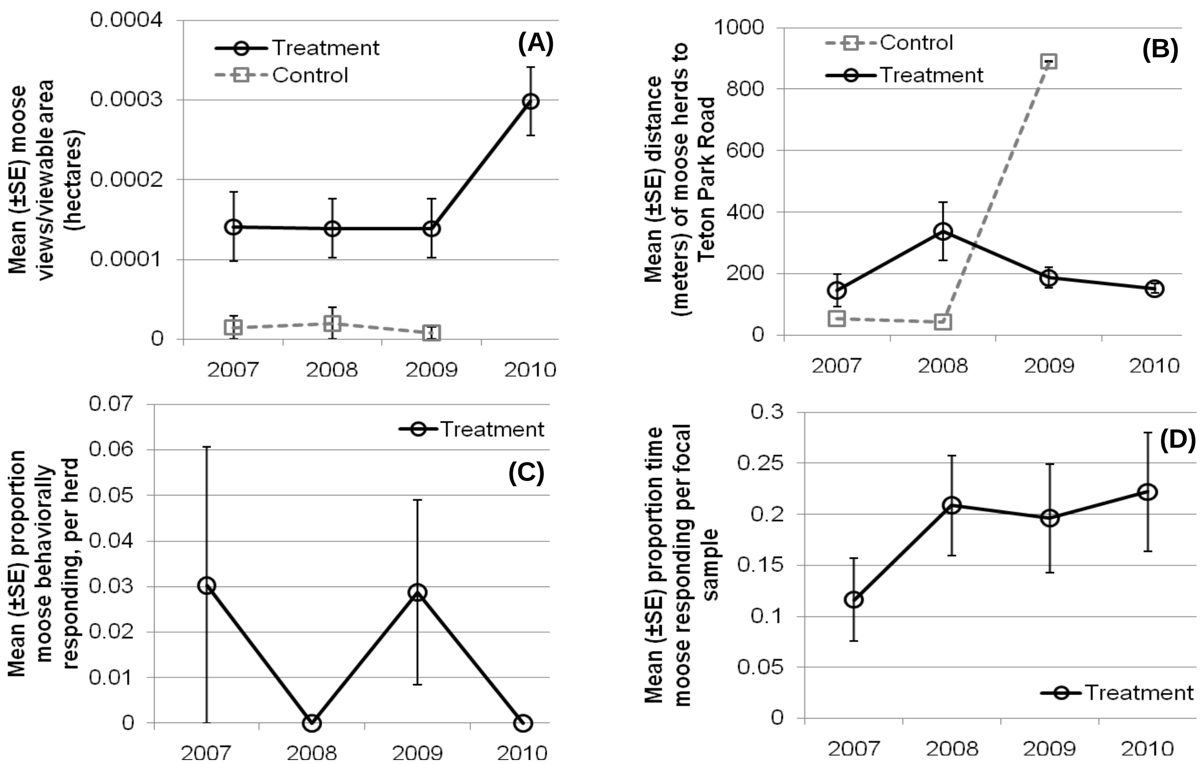

Figure 8. Annual mean (± standard error) A) number moose viewed (standardized by viewable area) per survey, B) distance of moose from road per group, C) proportion of moose responding per group, and D) proportion time moose responded per focal sample in the control and treatment areas in Grand Teton National Park from June-October of 2007-2010.

<u>Elk</u> – We viewed 1,321 elk groups comprised of 12,256 individual elk observations in the treatment and control over the four years of the study (Table 4; Appendix Map 3). Elk groups seen from the road ranged between 1 to 128 individuals (mean±SE = 9.28±0.41). Results of quantitative analyses reviewed in the text below are limited to significant main effects and year*area interactions; all results are included in referenced tables.

Table 4. Summary of elk groups and number within groups observed at crepuscular and day periods in the control and treatment areas during 421 road surveys conducted in Grand Teton National Park between June-October 2007-2010.

	ELK									
YEAR	*CONTROL AREA*				*TREATMENT AREA*				*TOTAL GROUPS*	*TOTAL # SEEN*
	Crepuscular		Day		Crepuscular		Day			
	groups	# seen	groups	# seen	groups	# seen	groups	# seen		
2007	42	310	21	226	43	577	61	931	167	2084
2008	53	324	101	964	94	914	119	1255	367	3457
2009	54	319	90	536	139	1485	212	1756	495	4096
2010	44	158	32	232	7	828	139	1401	292	2619
2007-2010	193	1111	244	1958	283	3804	531	5343	1321	12256

Number of elk viewed — In early season, we observed more elk per survey during crepuscular periods (mean±SE=0.0199±0.0034/ha) compared to day periods (0.0122±0.0012/ha; Figure 9; see Table 5 for model outputs). Additionally, more elk were viewed in the control (0.0202±0.0028/ha) than in the treatment (0.0106±0.0011/ha) during early season (Table 5). Annual trends of number of elk viewed during early season also fluctuated significantly between years throughout the study area, increasing from 2007 (0.0158±0.0075/ha) to 2008 (0.0217±0.0042/ha) and decreasing in 2009 (0.0144±0.0017/ha) and 2010 (0.0099±0.0016/ha; Table 5). Annual trends in number of elk viewed also varied between the control and treatment as reflected by the significant year*area interaction in early season (Table 5); the number of elk viewed in the control significantly decreased between 2008 (0.0312±0.0072/ha) and 2010 (0.0088±0.0022/ha) while remaining relatively stable or increasing slightly in the treatment during the study (Table 6, Figure 9). In late season, the number of elk viewed in the study area per survey decreased annually (Table 5) from 2007 (0.0247±0.0062/ha) to 2008 (0.0204±0.0028), 2009 (0.0155±0.0030/ha) and 2010 (0.0121±0.0028/ha; Figure 9).

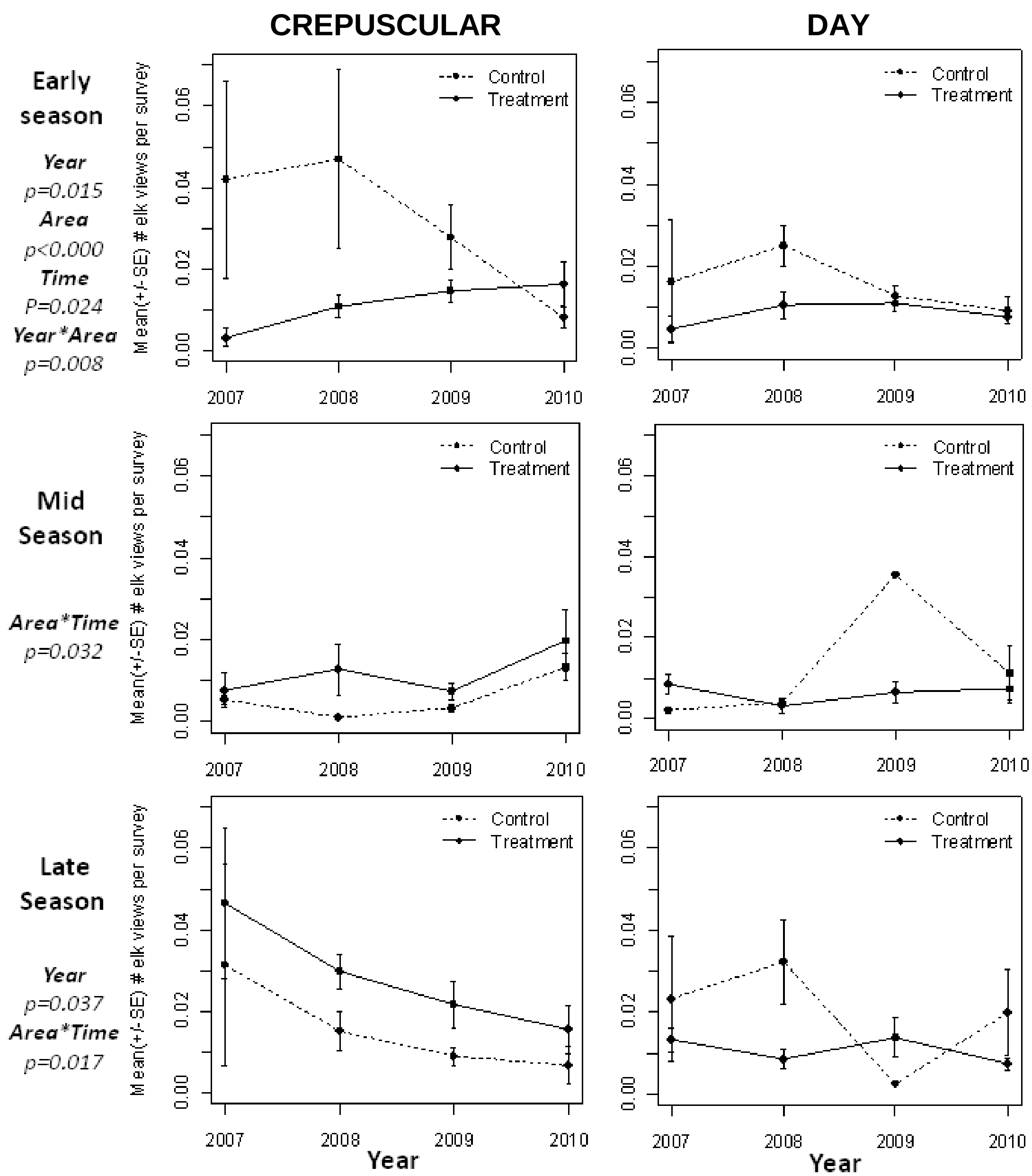

Figure 9. Annual mean (± standard error) number of elk viewed (standardized by viewable area) by season and time of day in the control and treatment areas per road survey, and model-derived significant effects by season, in Grand Teton National Park during June-October of 2007-2010.

Table 5. Main and interactive effects influencing mean number of elk viewed/viewable per road survey (n=421) over three seasons. Bold text highlights statistically significant (*p*<0.05) results (see Table 6 for post hoc analyses of significant interaction). Road surveys were conducted in Grand Teton National Park between June-October 2007-2010.

SEASON	*EFFECT*	*Between survey DF*	*Within survey DF*	*F-Value*	*P-value*
Early (June-July15)	**YEAR**	**3**	**93**	**3.692**	**0.015**
	AREA	**1**	**97**	**14.819**	**0.000**
	YEAR*AREA	**3**	**93**	**4.152**	**0.008**
	TIME	**1**	**97**	**5.280**	**0.024**
	YEAR*TIME	3	93	0.283	0.837
	AREA*TIME	1	97	1.500	0.224
	YEAR*AREA*TIME	3	93	0.971	0.410
Mid (July 16-Aug 31)	YEAR	3	86	2.215	0.092
	AREA	1	86	0.038	0.845
	YEAR*AREA	3	86	1.535	0.211
	TIME	1	86	0.007	0.932
	YEAR*TIME	3	86	2.600	0.057
	AREA*TIME	**1**	**86**	**4.763**	**0.032**
	YEAR*AREA*TIME	3	86	1.749	0.163
Late (Sept-Oct 15)	**YEAR**	**3**	**84**	**2.959**	**0.037**
	AREA	1	65	0.840	0.363
	YEAR*AREA	3	65	1.362	0.262
	TIME	1	85	3.110	0.081
	YEAR*TIME	3	84	1.163	0.329
	AREA*TIME	**1**	**65**	**5.977**	**0.017**
	YEAR*AREA*TIME	3	65	2.343	0.081

Table 6. Post hoc contrasts exploring the significant early season year*area interaction in Table 5. Bold text highlights statistically significant (*p*<0.05) results.

SEASON	*AREA*	*YEARS CONTRASTED A*	*B*	*CONTRAST ESTIMATE (A-B)*	*SE*	*DF*	*T-value*	*Tukey HSD P-value*
Early (June-July15)	CONTROL	2007	2008	-0.028	0.029	158	-0.950	0.778
		2007	2009	0.008	0.028	158	0.280	0.992
		2007	2010	0.053	0.029	158	1.852	0.256
		2008	2009	0.036	0.018	158	1.937	0.220
		2008	**2010**	**0.081**	**0.020**	**158**	**4.158**	**0.000**
		2009	2010	0.046	0.018	158	2.558	0.058
	TREATMENT	2007	2008	-0.041	0.024	158	-1.697	0.331
		2007	2009	-0.050	0.022	158	-2.277	0.111
		2007	2010	-0.041	0.023	158	-1.796	0.282
		2008	2009	-0.010	0.017	158	-0.566	0.942
		2008	2010	0.000	0.018	158	-0.007	1.000
		2009	2010	0.010	0.015	158	0.624	0.924

Elk distance from road — We measured distance from road for 1,304 elk groups seen during 421 road surveys (Figure 10). Time of day influenced the distance at which we observed elk groups from the road over all seasons (Table 7). Elk were seen 218m, 329 m and 470m farther from the road during day surveys compared to crepuscular surveys in early, mid and late seasons, respectively. During early season, elk distances from the road fluctuated significantly over the years of the study (Table 7), increasing from 2007 (mean±SE=341.3±48.7) to 2008 (580.6±32.2m) and 2009 (783.4±31.7m), and decreasing in 2010 (560.5±33.4m). During mid season, elk groups were seen progressively farther from the road each year of the study (Table 7), from 2007 (438.9±81.8m) to 2008 (558.6±52.4m), 2009 (620.2±58.26m), and 2010 (694.1±60.4m). During late season, elk were, on average, seen about 418m farther from the road in the treatment (745.4±37.3m) compared to the control (327.7±30.8m). Despite these effects, no significant year*area interactions emerged (Table 7); annual trends were similar in the treatment and control areas.

Table 7. Main and interactive effects influencing mean elk group distance from the road over three seasons Bold text highlights statistically significant (*p*<0.05) results. Group distance data were recorded during 421 road surveys conducted in Grand Teton National Park between June-October 2007-2010.

SEASON	*EFFECT*	*Between groups DF*	*Within groups DF*	*F-Value*	*P-value*
Early (June-July15)	**Year**	**3**	**173**	**8.440**	**0.000**
	Area	1	217	0.420	0.518
	Year*Area	3	173	1.771	0.154
	Time	**1**	**364**	**9.927**	**0.002**
	Year*Time	3	287	2.589	0.053
	Area*Time	1	364	0.011	0.915
	Year*Area*Time	3	287	1.323	0.267
Mid (July 16-Aug 31)	**Year**	**3**	**151**	**4.766**	**0.003**
	Area	1	163	2.611	0.108
	Year*Area	3	151	2.114	0.101
	Time	**1**	**196**	**9.245**	**0.003**
	Year*Time	3	193	0.955	0.415
	Area*Time	1	196	0.697	0.405
	Year*Area*Time	3	193	0.435	0.728
Late (Sept-Oct 15)	Year	3	144	0.647	0.586
	Area	**1**	**155**	**25.899**	**0.000**
	Year*Area	3	144	0.410	0.746
	Time	**1**	**205**	**26.070**	**0.000**
	Year*Time	3	202	0.604	0.613
	Area*Time	1	205	1.236	0.267
	Year*Area*Time	3	202	0.292	0.831

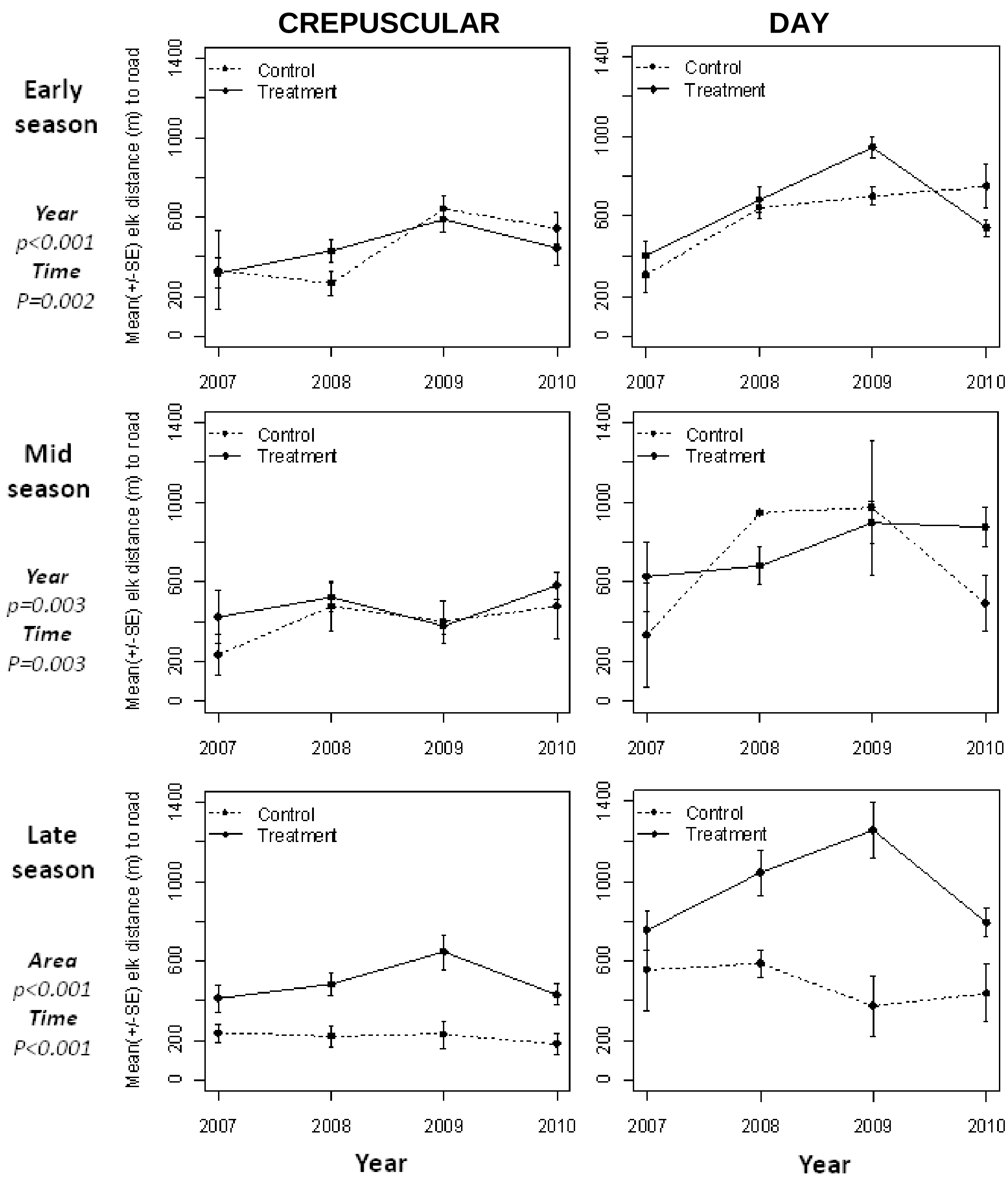

Figure 10. Annual mean (± standard error) elk group distance (meters) from the road by season and time of day in the control and treatment areas, with model-derived significant effects by season, in Grand Teton National Park during June-October of 2007-2010.

Elk group scan responsiveness – During 421 road surveys, we recorded behavior scans on 419 elk groups, accounting for 3,722 elk behavior observations (Figure 11). In early season, we detected no significant main or interactive effects (Table 8). In mid seasons, we conducted behavior scans on 2, 3, and 8 elk groups in the control area in 2008, 2009 and 2010, respectively, with no elk observed responding (Figure 11). Similarly, in late seasons, we recorded scan samples where no elk responded in 6 and 8 groups in the control in 2009 and 2010, respectively (Figure 11). Low sample sizes, however, precluded statistical analyses for these seasons.

Table 8. Main and interactive effects influencing probability of individual elk responding per group during early seasons. Elk group behavior scan data were recorded during 421 road surveys conducted in Grand Teton National Park between June-October 2007-2010.

SEASON	*EFFECT*	*Between groups DF*	*Within groups DF*	*F-Value*	*P-value*
Early (June-July15)	YEAR	3	28	0.701	0.559
	AREA	1	15	1.466	0.244
	YEAR*AREA	3	15	1.850	0.182
	TIME	1	55	1.946	0.169
	YEAR*TIME	3	56	0.343	0.794
	AREA*TIME	1	105	1.413	0.237
	YEAR*AREA*TIME	3	103	0.438	0.726

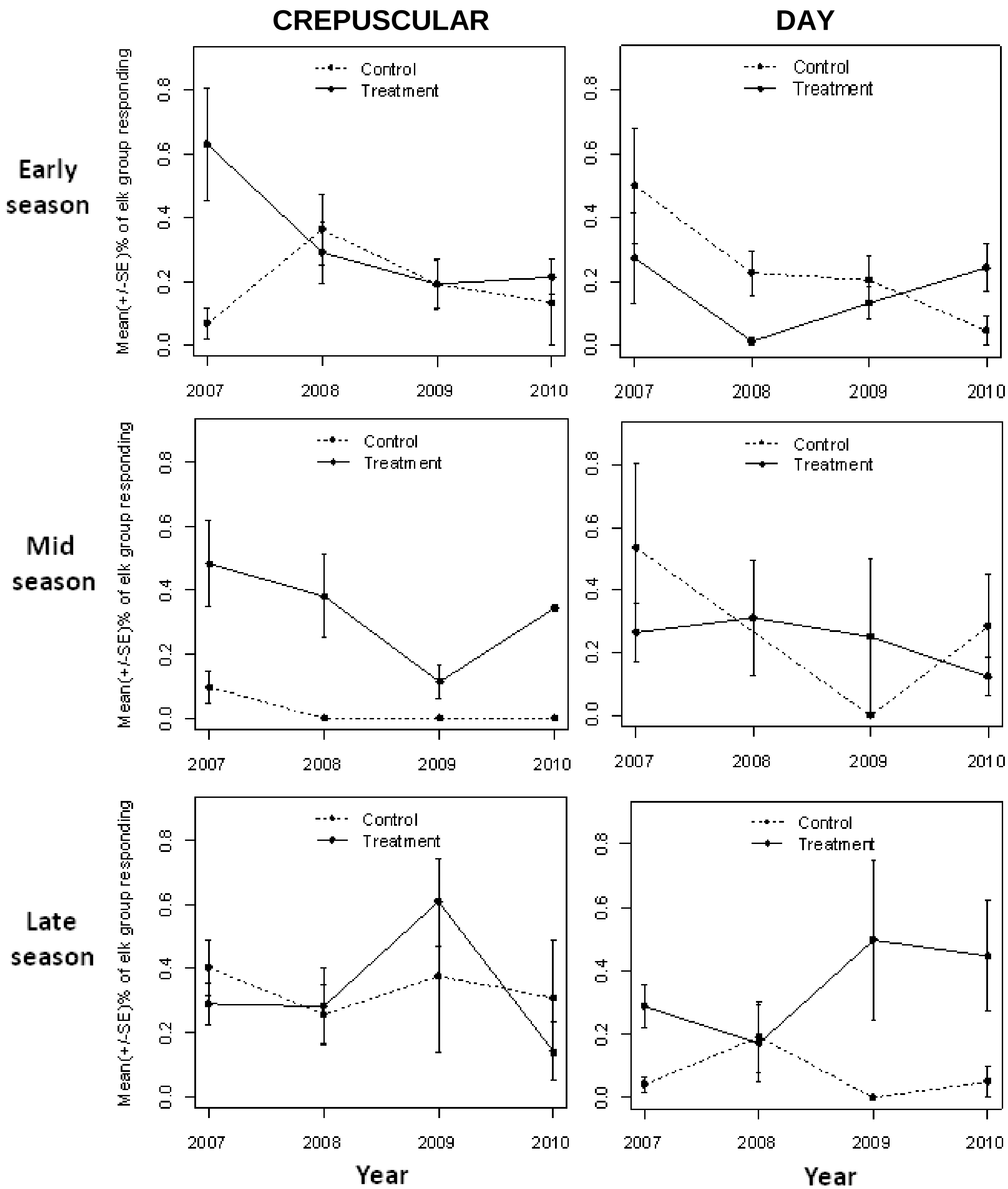

Figure 11. Annual mean (± standard error) proportion of elk per group observed behaviorally responding by season and time of day in the control and treatment area, and model-derived significant effects by season, in Grand Teton National Park during June-October of 2007-2010.

Elk focal sample responsiveness – We conducted 330 elk focal samples, recording 78 hours of focal elk behavior data over the four years of the study (Figure 12). In early season, the probability of an elk responding was higher during crepuscular periods (mean±SE=0.231±0.037) than day periods (0.165±0.030; Table 9). The three-way interaction year*area*time was significant (Table 9); post hoc tests analyzing the effect of year, area and year*area by crepuscular and day observation times separately, yielded no further significant results (Table 10), indicating that time of day was the driver of the significant three-way interaction. In mid season, annual trends in responsiveness varied between control and treatment as represented by the significant year*area interaction (Table 9). However, post hoc annual contrasts failed to find significant differences between years (Table 11), likely due to high variability in these estimates and conservative adjusted *p*-values associated with the Tukey's multiple comparison test. Effect plots suggest that behavioral responsiveness in elk in the treatment decreased while increasing in the control, particularly during mid season crepuscular periods (Figure 12).

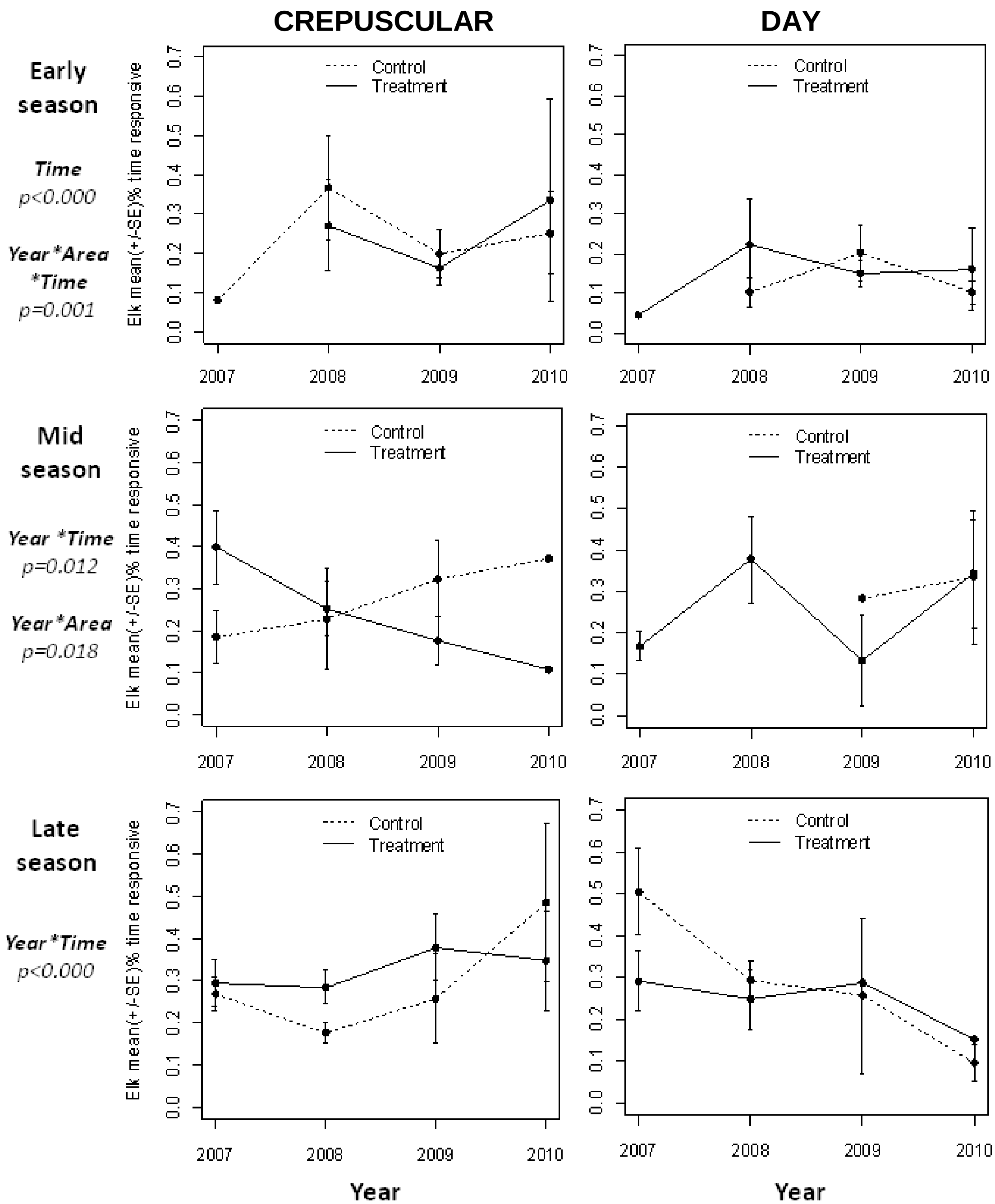

Figure 12. Annual mean (± standard error) percent time elk responded per focal sample, by season and time of day in the control and treatment areas, with model-derived significant effects by season, in Grand Teton National Park from June-October of 2007-2010.

Table 9. Main and interactive effects influencing probability of an elk responding per second during 330 elk focal sample collected in the control and treatment areas over three seasons. Bold text highlights statistically significant (*p*<0.05) results (see Tables 10, 11 for post hoc analyses of significant interactions). Focal samples were collected in Grand Teton National Park between June-October 2007-2010.

SEASON	*EFFECT*	*Between sample DF*	*Within sample DF*	*F-Value*	*P-value*
Early (June-July15)	YEAR	3	24	0.376	0.771
	AREA	1	27	0.013	0.910
	YEAR*AREA	2	27	0.012	0.988
	TIME	**1**	**42**	**16.500**	**0.000**
	YEAR*TIME	2	43	2.447	0.099
	AREA*TIME	1	40	0.085	0.772
	YEAR*AREA*TIME	**2**	**41**	**7.850**	**0.001**
Mid (July 16-Aug 31)	YEAR	3	41	0.086	0.967
	AREA	1	41	0.320	0.575
	YEAR*AREA	**3**	**27**	**4.012**	**0.018**
	TIME	1	44	1.000	0.323
	YEAR*TIME	**3**	**45**	**4.106**	**0.012**
	AREA*TIME	1	45	0.209	0.650
	YEAR*AREA*TIME	1	45	0.507	0.480
Late (Sept-Oct 15)	YEAR	3	68	0.692	0.560
	AREA	1	81	0.089	0.767
	YEAR*AREA	3	67	1.453	0.235
	TIME	1	92	0.001	0.981
	YEAR*TIME	**3**	**169**	**8.851**	**0.000**
	AREA*TIME	1	92	0.123	0.727
	YEAR*AREA*TIME	3	171	1.659	0.178

Table 10. Post hoc analysis of the significant early season three-way interaction (see Table 9) for the probability of an elk responding per second of a focal sample, dropping time from the model to assess effects at crepuscular and day periods separately.

EFFECT	*Between sample DF*	*Within sample DF*	*F-Value*	*P-value*
EARLY SEASON, CREPUSCULAR				
YEAR	3	17	0.784	0.519
AREA	1	8	0.016	0.903
YEAR*AREA	2	8	0.026	0.974
EARLY SEASON, DAY				
YEAR	3	22	0.236	0.870
AREA	1	18	0.227	0.639
YEAR*AREA	2	12	0.355	0.709

Table 11. Post hoc contrasts of annual year*area interactions (see Table 9) by area for midseason elk probabilities of responding per second during focal samples.

AREA	*YEARS CONTRASTED* *A*	*B*	*CONTRAST ESTIMATE (A-B)*	*SE*	*DF*	*T-value*	*Tukey's HSD P-value*
CONTROL	2007	2008	Inestimable contrasts (high variability)				
	2007	2009					
	2007	2010					
	2008	2009					
	2008	2010					
	2009	2010	0.161	1.055	44	0.153	0.879
TREATMENT	2007	2008	-0.046	0.534	44	-0.087	1.000
	2007	2009	1.206	0.583	46	2.070	0.189
	2007	2010	0.446	0.834	44	0.535	0.950
	2008	2009	1.252	0.591	45	2.119	0.173
	2008	2010	0.493	0.840	43	0.586	0.935
	2009	2010	-0.760	0.872	44	-0.871	0.820

Pronghorn antelope –Over the duration of the study, we saw 734 groups of pronghorn containing 2,055 individual pronghorn observations (Table 12; Appendix Map 4). Pronghorn groups ranged in size from 1-22 individuals (mean±SE =2.79±0.1); most (>95%) pronghorn groups contained <10 animals.

Table 12. Summary of pronghorn antelope groups and number within groups observed at crepuscular and day periods in the control and treatment areas during 421 road surveys conducted in Grand Teton National Park between June-October 2007-2010.

	PRONGHORN ANTELOPE									
	CONTROL AREA				*TREATMENT AREA*					
YEAR	Crepuscular		Day		Crepuscular		Day		*TOTAL GROUPS*	*TOTAL # SEEN*
	groups	# seen	groups	# seen	groups	# seen	groups	# seen		
2007	3	8	5	12	12	79	40	191	60	290
2008	12	40	48	127	17	87	71	271	148	525
2009	10	33	45	104	51	111	205	484	311	732
2010	13	38	66	112	21	64	115	294	215	508
2007-2010	38	119	164	355	101	341	431	1240	734	2055

Number of pronghorn viewed – During early season, the number of pronghorn viewed per survey varied significantly over years (Figure 13, Table 13); we saw the fewest pronghorn per survey in 2007 (mean±SE=0.0025±0.0006/ha), the most in 2008 (0.0048±0.0005/ha), with moderate numbers in 2009 (0.0037±0.0003/ha) and 2010 (0.0026±0.0003/ha). The number of pronghorn viewed was significantly higher in the control (0.0043±0.0004/ha) than in the treatment area (0.0030±0.0002/ha; Table 13). Post hoc tests exploring the significant early season three-way interaction, analyzing crepuscular and day observations separately, did not reveal any significant year*area interactions (Table 14). During early season crepuscular periods, we saw significantly more pronghorn in the control (0.0052 ± 0.0008/ha) than in the treatment (0.0029±0.0004/ha). During day surveys, the number of pronghorn viewed across both the control and treatment areas together was lowest in 2007 (mean±SE= 0.0019±0.0004/ha), peaked in 2008 (0.0048± 0.0006/ha), and was intermediate in 2009 (0.0038±0.0004/ha) and 2010 (0.0023±0.0003/ha). In late season, we saw the most pronghorn in 2007 (0.0043±0.0005/ha), dropping in 2008 (0.0037±0.0006/ha) and 2009 (0.0015±0.0004/ha), and increasing in 2010 (0.0025±0.0004/ha; Table 13). There were no significant year*area interactions (Table 13), suggestive of no pathway impact.

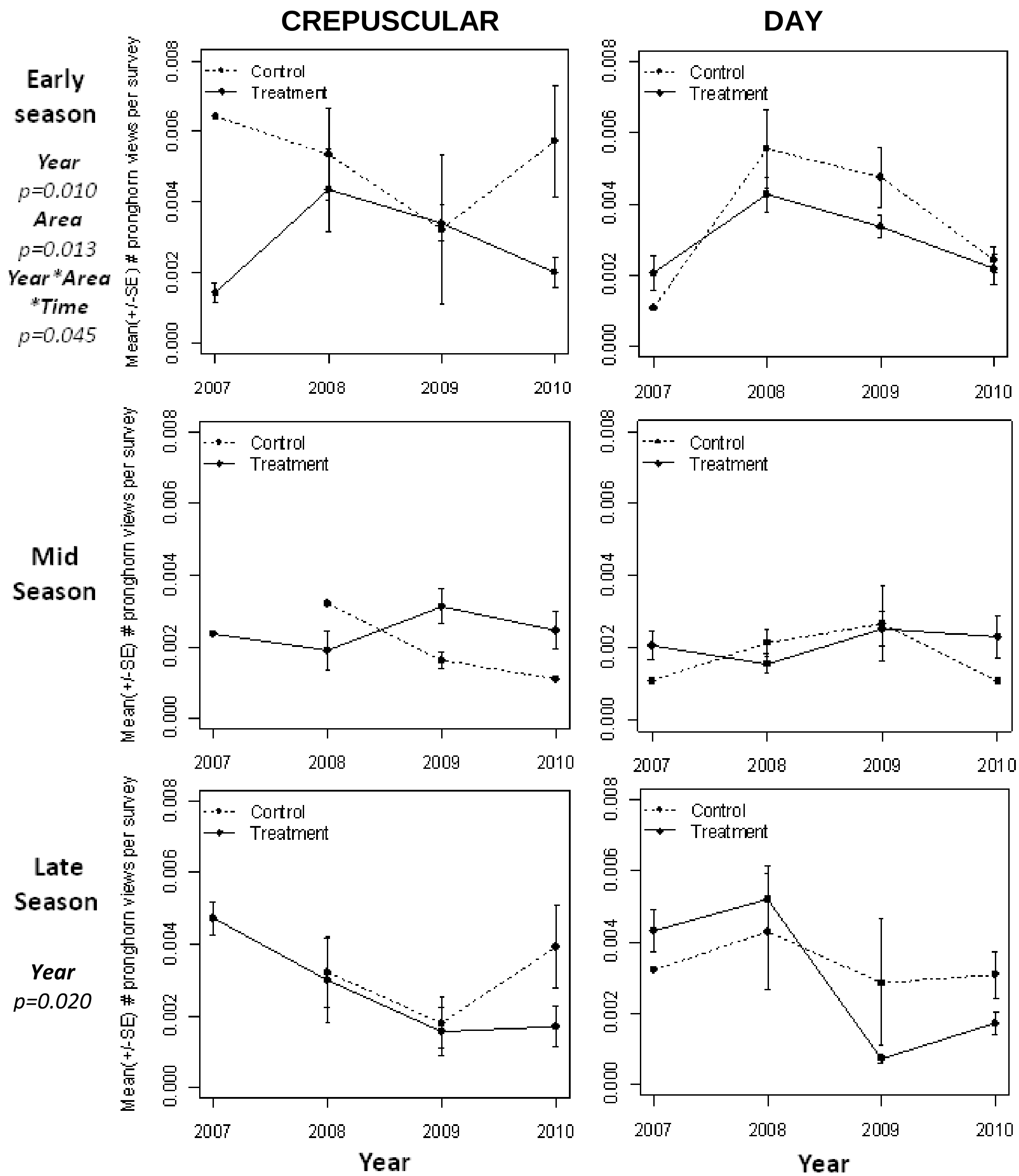

Figure 13. Annual mean (± standard error) number of pronghorn viewed (standardized by viewable area) by season and time of day in the control and treatment areas per road survey, with model-derived significant effects by season, in Grand Teton National Park during June-October of 2007-2010.

Table 13. Main and interaction effects influencing numbers of pronghorn viewed (standardized by viewable area) from the Teton Park Road in the control and treatment areas per road survey over three seasons. Bold text highlights statistically significant (*p*<0.05) results (see Table 14 for post hoc analyses of significant interaction). Road surveys were conducted in Grand Teton National Park between June-October 2007-2010.

SEASON	*EFFECT*	*Between survey DF*	*Within survey DF*	*F-Value*	*P-value*
Early (June-July15)	**YEAR**	**3**	**121**	**3.912**	**0.010**
	AREA	**1**	**110**	**6.325**	**0.013**
	YEAR*AREA	3	101	1.309	0.276
	TIME	1	130	1.642	0.202
	YEAR*TIME	3	121	1.906	0.132
	AREA*TIME	1	110	3.276	0.073
	YEAR*AREA*TIME	**3**	**101**	**2.771**	**0.045**
Mid (July 16-Aug 31)	YEAR	3	88	1.367	0.258
	AREA	1	89	0.849	0.359
	YEAR*AREA	3	76	1.290	0.284
	TIME	1	94	0.495	0.483
	YEAR*TIME	3	88	0.182	0.909
	AREA*TIME	1	86	0.169	0.682
	YEAR*AREA*TIME	2	70	0.520	0.597
Late (Sept-Oct 15)	**YEAR**	**3**	**71**	**3.483**	**0.020**
	AREA	1	74	2.358	0.129
	YEAR*AREA	3	53	1.310	0.281
	TIME	1	73	0.106	0.746
	YEAR*TIME	3	71	1.426	0.242
	AREA*TIME	1	47	0.002	0.960
	YEAR*AREA*TIME	2	40	1.364	0.267

Table 14. Post hoc analysis of the significant early season three-way interaction (see Table 13) effect on pronghorn viewed, dropping time from the model to assess effects at crepuscular and day periods separately.

EFFECT	*between survey DF*	*within survey DF*	*F-Value*	*P-value*
EARLY SEASON, CREPUSCULAR OBSERVATIONS				
YEAR	3	29	0.743	0.535
AREA	**1**	**29**	**7.000**	**0.013**
YEAR*AREA	3	28	2.147	0.117
EARLY SEASON, DAY OBSERVSATIONS				
YEAR	**3**	**85**	**7.703**	**0.000**
AREA	1	79	0.334	0.565
YEAR*AREA	3	67	0.288	0.834

Pronghorn distance from road —During early season, pronghorn were farther from the road in the control (mean±SE=443.4±33.1m) than in the treatment (355.7±21.5m; Figure 14). In mid season, pronghorn observations during the day were, on average, farther from the road (308.6±22.7m) than groups observed during crepuscular periods (216.5±28.4m; Table 15). Additionally, during mid season, annual trends in pronghorn distance from road in the treatment and control diverged as indicated by the significant year*area interaction (Table 15). Post hoc contrasts (Table 16) confirm that, during mid season, pronghorn were observed about 164m farther from the road in the treatment in 2010 (366.9±50.2m) than 2007 (202.2±35.3m), while pronghorn shifted, on average, about 181m closer to the road in the control in 2010 (408.9±69.7m) compared to 2009 (228.2±63.9m).

Table 15. Main and interactive effects influencing mean pronghorn distances from the Teton Park Road over three seasons. Bold text highlights statistically significant (*p*<0.05) results (see Table 16 for post hoc analyses of significant interaction). Pronghorn distances to road were collected during road surveys conducted in Grand Teton National Park between June-October 2007-2010.

SEASON	*EFFECT*	*Between groups DF*	*Within groups DF*	*F-Value*	*P-value*
Early (June-July15)	YEAR	3	295	0.498	0.684
	AREA	**1**	**359**	**4.123**	**0.043**
	YEAR*AREA	3	294	1.128	0.338
	TIME	1	372	2.223	0.137
	YEAR*TIME	3	303	1.212	0.306
	AREA*TIME	1	256	0.053	0.818
	YEAR*AREA*TIME	2	255	0.388	0.679
Mid (July 16-Aug 31)	YEAR	3	130	1.030	0.382
	AREA	1	162	0.264	0.608
	YEAR*AREA	**3**	**161**	**5.137**	**0.002**
	TIME	**1**	**145**	**6.330**	**0.013**
	YEAR*TIME	3	136	0.554	0.646
	AREA*TIME	1	162	1.083	0.300
	YEAR*AREA*TIME	2	160	0.412	0.663
Late (Sept-Oct 15)	YEAR	3	83	0.031	0.993
	AREA	1	101	2.082	0.152
	YEAR*AREA	3	98	2.034	0.114
	TIME	1	95	2.705	0.103
	YEAR*TIME	3	93	0.604	0.614
	AREA*TIME	1	98	0.042	0.838
	YEAR*AREA*TIME	2	96	1.020	0.365

Table 16. Post hoc annual contrasts of the mid season year*area interaction effects (see Table 15) on pronghorn group distance from road.

SEASON	AREA	YEARS A	YEARS B	CONTRAST (A-B)	SE	DF	T-value	Tukey HSD P-value
Mid (July 16-Aug 31)	CONTROL	2007	2008	Inestimable contrast due to low sample size: n=2 observations in the control in 2007 mid season during midday				
		2007	2009					
		2007	2010					
		2008	2009	-5.049	2.519	156	-2.005	0.114
		2008	2010	1.664	2.683	159	0.620	0.809
		2009	**2010**	**6.713**	**2.623**	**161**	**2.560**	**0.030**
	TREATMENT	2007	2008	-2.863	3.471	158	-0.825	0.843
		2007	2009	-3.045	1.804	107	-1.688	0.333
		2007	**2010**	**-5.185**	**1.958**	**112**	**-2.649**	**0.044**
		2008	2009	-0.182	3.267	156	-0.056	1.000
		2008	2010	-2.322	3.354	155	-0.692	0.900
		2009	2010	-2.140	1.567	70	-1.365	0.523

Pronghorn group scan responsiveness – We conducted 412 behavior scans on pronghorn groups during the four years of the study. High variability in pronghorn group scan observations (Figure 15) combined with low sample sizes in some years precluded statistical analyses in early and mid season. No significant main or interactive effects were evident for the late season (Table 17). Graphical examination also do not suggest any clear pathway impact (Figure 15).

Table 17. Main and interaction effects influencing percent of pronghorn behaviorally responding, per group scan observation, during road surveys on Teton Park Road during late season. Road surveys were conducted in Grand Teton National Park during June-October 2007-2010.

EFFECT: Late Season (Sept-Oct 15)	Between groups DF	Within groups DF	F-Value	P-value
YEAR	3	35	1.19535	0.3256
AREA	1	46	0.10097	0.7521
YEAR*AREA	2	44	0.10655	0.8992
TIME	1	43	0.23243	0.6322
YEAR*TIME	3	35	1.71596	0.1813
AREA*TIME	1	46	0.18185	0.6718
YEAR*AREA*TIME	2	44	0.03956	0.9612

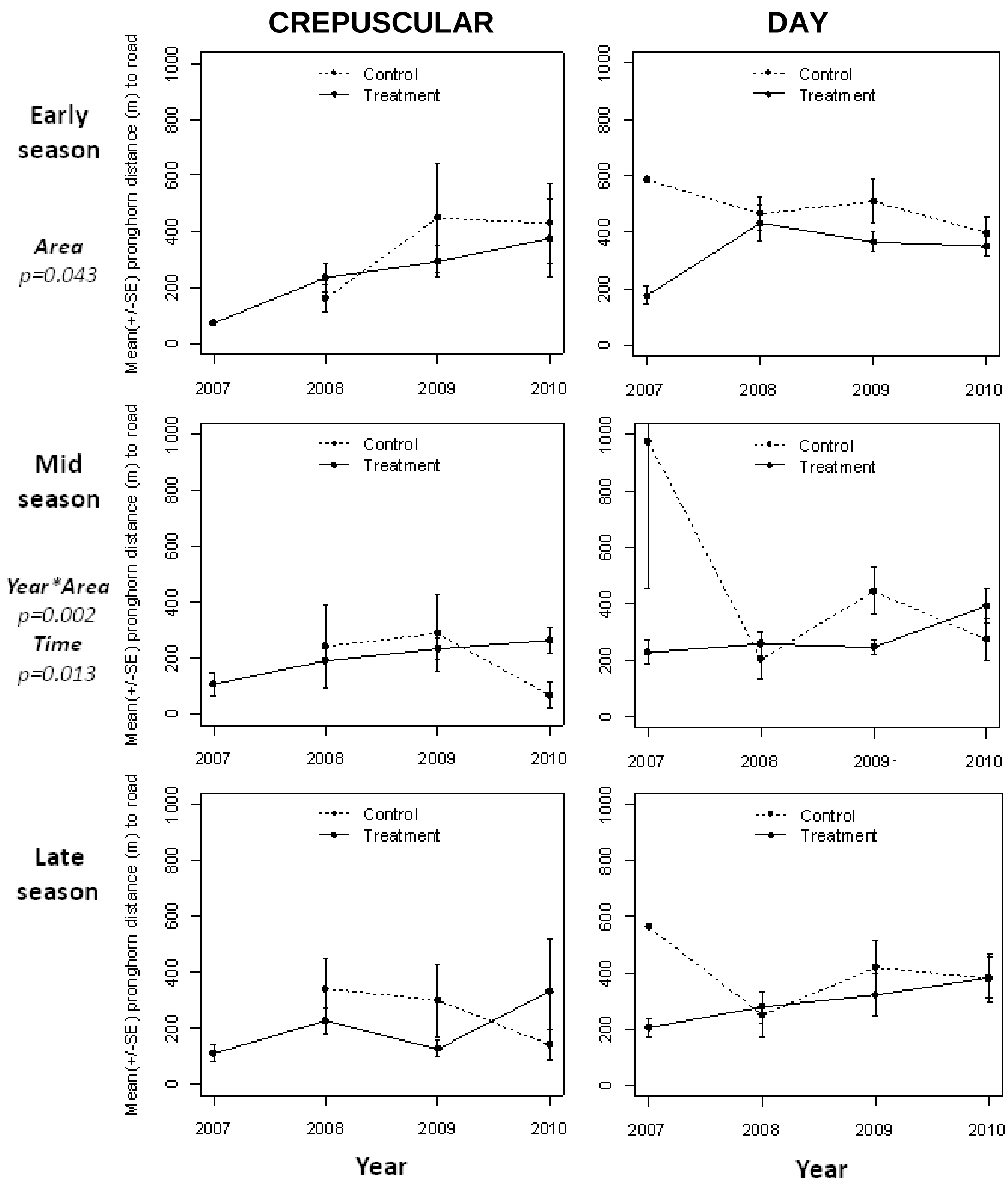

Figure 14. Annual mean (± standard error) pronghorn antelope group distances (meters) to road by season and time of day in the control and treatment areas, with model-derived significant effects by season, in Grand Teton National Park during June-October of 2007-2010.

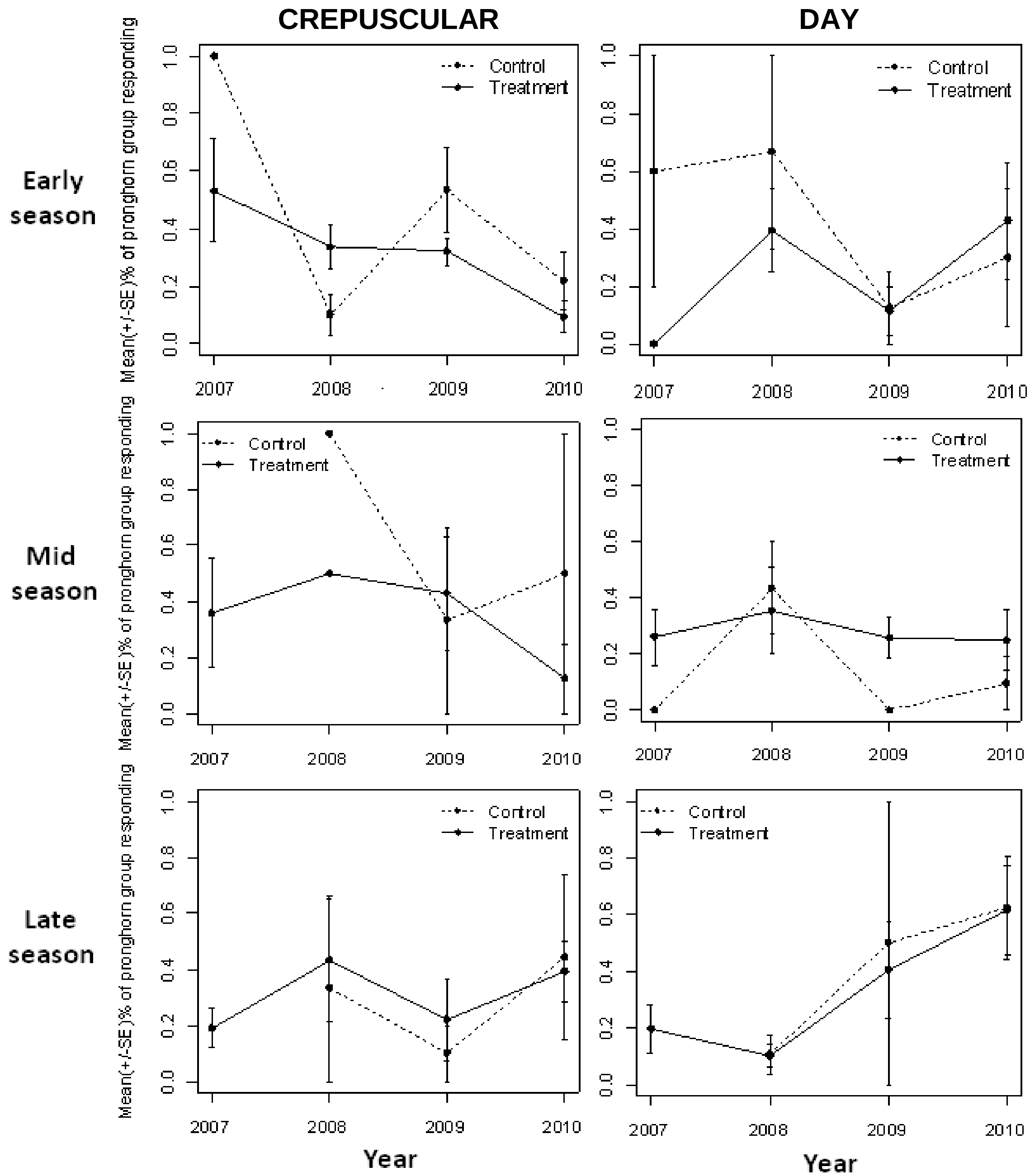

Figure 15. Annual mean (± standard error) proportion of pronghorn observed behaviorally responding per group by season and time of day in the control and treatment area in Grand Teton National Park during June-October of 2007-2010.

Pronghorn focal sample responsiveness – We conducted 251 focal samples on pronghorn, obtaining more than 53 hours of observation time during the study. Analyses for all seasons revealed no significant effects (Table 18). Graphical examination of mean proportion of time pronghorn responded per focal sample also does not suggest a clear pathway impact (Figure 16).

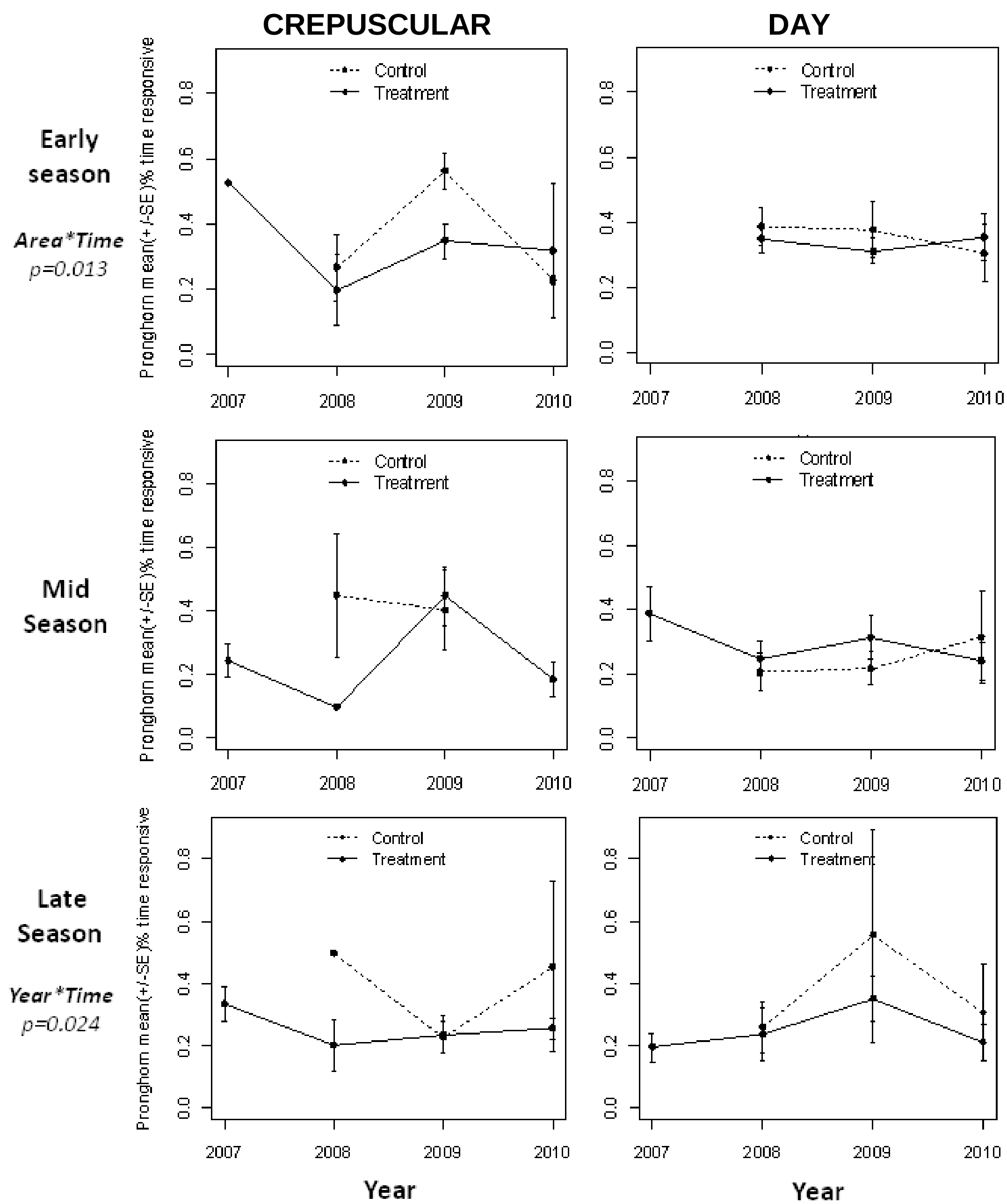

Figure 16. Annual mean (± standard error) percent time pronghorn responded per focal sample, by season and time of day in the control and treatment areas, with model-derived significant effects by season, in Grand Teton National Park from June-October of 2007-2010.

Table 18. Main and interaction effects influencing pronghorn percent time responding per focal behavior sample over three seasons. Bold text highlights statistically significant (p<0.05) effects.

SEASON	EFFECT	Between sample DF	Within sample DF	F-Value	P-value
Early (June-July15)	YEAR	3	67	0.791	0.503
	AREA	1	57	0.548	0.462
	YEAR*AREA	2	56	2.339	0.106
	TIME	1	73	1.831	0.180
	YEAR*TIME	2	74	0.513	0.601
	AREA*TIME	**1**	**71**	**6.481**	**0.013**
	YEAR*AREA*TIME	2	72	0.783	0.461
Mid (July 16-Aug 31)	YEAR	3	56	0.738	0.534
	AREA	1	56	0.914	0.343
	YEAR*AREA	2	56	0.558	0.576
	TIME	1	57	0.507	0.480
	YEAR*TIME	3	59	2.509	0.068
	AREA*TIME	1	56	0.984	0.325
	YEAR*AREA*TIME	1	56	1.421	0.238
Late (Sept-Oct 15)	YEAR	3	36	0.152	0.928
	AREA	1	28	2.216	0.148
	YEAR*AREA	2	28	0.137	0.873
	TIME	1	40	0.009	0.925
	YEAR*TIME	**3**	**40**	**3.496**	**0.024**
	AREA*TIME	1	36	0.229	0.635
	YEAR*AREA*TIME	2	35	3.182	0.054

DISCUSSION

The new multi-use pathway along Teton Park Road (TPR) resulted in direct habitat loss, construction disturbance and changes in human activities along the transportation corridor in Grand Teton National Park. Our results, however, did not clearly or consistently demonstrate that ungulate distribution and behavior, or wildlife viewing opportunities, were considerably affected by the construction and use of the pathway. The strongest evidence of an ungulate avoidance response to the pathway included a relatively modest shift in pronghorn distribution away from the road and path corridor during periods of peak visitation and pathway use. Additionally, elk behavioral responsiveness during peak visitation appeared to decrease in the treatment relative to the control, particularly during crepuscular hours, potentially suggestive of elk tolerance to activities in the treatment. Ultimately, park visitors could still view these species from the TPR during pathway construction and after the pathway opened.

Although automobile traffic volumes did not change over the duration of the study (Sawyer et al. 2011), the installation of the pathway increased and diversified non-motorized travel activities in the TPR corridor, meeting a stated objective of the park transportation plan (National Park Service 2006). With the opening of the pathway, most pedestrian and bicyclist activities shifted from the road to the pathway and we estimated a concurrent ~3 fold increase in bicycling activity. Infrared trail counters detected as many as 148 pathway users passing on the pathway per hour, peaking seasonally between June 15 and August 30, and daily between 1100 and 1600 hours (Costello et al. 2011). This shift in non-motorized travel from the road to the pathway presumably decreased the potential for collisions and conflicts between automobiles and pedestrians and bicyclists, meeting another stated objective of the transportation plan (National Park Service 2006). However, the overall increase in non-motorized travelers since the pathway opened could potentially increase interactions and possibly conflicts between wildlife and park visitors. This may be particularly true considering the three-fold increase in off-road and off-trail travel in the treatment since pathway construction. Previous research demonstrates ungulates are more likely to respond to off-road and off-path activities than the more frequent but predictable activities that occur on linear infrastructure (MacArthur et al. 1979, Cassirer et al. 1992, Knight and Cole 1995, Miller et al. 2001, Papouchis et al. 2001, Borkowski et al. 2006).

Wildlife viewing opportunities did not seem to be substantially impacted by the pathway. Even prior to the completion of pathway construction in 2008, people ventured from the road to watch wildlife from the pathway at 3% of our sampling sites, and we measured a four-fold increase in wildlife viewing from the pathway once it opened to the public. We documented people watching wildlife from the road at more than 50% of our sampling points in the treatment area in 2008, decreasing to a quarter of our sampling points in 2009, and recovering in 2010 to a level similar to that seen in 2008. In the control, by comparison, we witnessed people viewing wildlife from the road at 34% of survey scan points in 2008, when ungulate observations in the control peaked, but wildlife viewing dropped to 5% and 3.5% of the control scan points in 2009 and 2010, coinciding with a decrease in ungulate observations in the control (discussed below). The fact wildlife viewing in the treatment in 2010 was similar to 2008 indicates that the pathway did not have a considerable impact on visitor opportunities to see ungulates from the road. A concurrent study assessing elk habitat use and movements based on fine-scale GPS data from a sample of individual elk occupying the pathway study area indicated that high-use elk habitats visible from the TPR did not noticeably change before, during and two years after pathway construction (Sawyer et al. 2011). This corroborates our finding that opportunities to view ungulates (elk, in particular) from the TPR did not change noticeably with the onset of pathway construction and use, and foreshadows our findings of few detectable changes in ungulate distribution which may be attributed to pathway activities.

If ungulates were avoiding pathway activities, we predicted a decreasing trend in the number of ungulates seen per survey in the treatment compared to the control after pathway construction. Our results do not support this prediction. For elk, we did not find statistical evidence for a decrease in elk numbers or displacement away from the road in the treatment compared to the control during the study. The only statistically significant year*area interaction, indicative of a pathway impact in our BACI experimental design, was a decrease in the number of elk viewed in the control between 2008 and 2010 during early season, while the number in the treatment area did not significantly change over the same period. This lack of a pathway effect is again consistent with findings from the concurrent study of GPS-collared elk that concluded that elk movement, habitat use and crossings of the TPR were not affected by pathway construction or use (Sawyer et al. 2011). We also predicted that we would see increased behavioral responsiveness in the treatment compared to the control if the pathway induced an avoidance response in ungulates. Again, contrary to this prediction, during the mid season when visitation peaked, elk behavioral responsiveness during crepuscular periods appeared to decrease in the treatment relative to the control over the duration of the study. Based on these outcomes, it was not apparent that elk avoided the pathway or were substantially disturbed by human activities occurring in the treatment during and after the construction of the pathway. Rather, it appears elk may have been tolerant of human activities, including pathway construction and use in the treatment.

Our results suggest that pronghorn may have avoided pathway activities by shifting away from the TPR in the treatment. Specifically, in mid season, during peak visitation, pronghorn were seen about 164 meters farther from the road in the treatment in 2010 compared to 2007, although they were seen 97 meters closer, on average, to the road in the control region in 2010 compared to 2009. This suggests that pronghorn may have been somewhat disturbed by construction and pathway activities, occupying areas farther from the road corridor after pathway construction. The estimated number of pronghorn viewed and measures of pronghorn behavioral responsiveness, however, were variable and not indicative of a pathway effect, although it is possible our methods failed to distinguish subtle pronghorn responses to pathway activities. Compared to elk, pronghorn are considered to be more sensitive to human disturbances, exhibiting risk-avoidance behavior in proximity to roads with traffic (Berger et al. 1983, Gavin and Komers 2006). A study of the effect of anthropogenic noise on elk and pronghorn in the same GTNP pathway study area in 2008 affirmed our findings of a higher level of behavioral responsiveness in pronghorn compared to elk (Brown et al. In review.). Despite the relative differences between elk and pronghorn responsiveness, both species were less likely to behaviorally respond as noise levels and vehicle traffic intensified, which, as reviewed below, potentially suggests habituation to such disturbances (Brown et al. In review.).

Compared to pronghorn and elk, far fewer mule deer were seen in the study area, comprising only 2% of all ungulate sightings. We saw mule deer during a quarter of our road surveys, and all but 9% of these observations were collected in the treatment area. Mean distances of mule deer groups to the road in the treatment ranged from 148m to 222 m during 2008 and 2009, respectively, with intermediate distances observed at the beginning and end of the study, offering no obvious pattern of avoidance of pathway construction or use. Behavioral responsiveness of mule deer was relatively infrequent and also not suggestive of a pathway impact. Mule deer often bedded within sight of the road along edges of forested cover, well-camouflaged and undetectable to most people on the road, as we observed many people pass by seemingly unaware of the mule deer viewing opportunity. Despite their infrequent appearance near the TPR, people were seen watching mule deer from the road during all four years of the study. Low sample sizes precluded statistical analyses of mule deer observations, but the fact that we continued to see mule deer in the treatment area during and after construction, with relatively little behavioral responsiveness to human disturbance, suggests that this species did not appear to be avoiding pathway activities.

Moose were observed the least often, comprising only 1% of all ungulate observations. Out of 421 road surveys, we saw only 4 moose in the control in the first three years of the study; no moose were seen in the control in 2010, when annual moose sightings peaked in the treatment (83 moose in 51 group observations; 41% of all moose observations). Moose were observed farther from the road in the treatment in 2008 compared to other years, with mean distances to the road decreasing to pre-pathway measurements by 2010. Although speculative, this may indicate a response to pathway construction, followed by increasing tolerance to human activities after the initial construction disturbance subsided and pathway use ensued. As with mule deer, behavioral responsiveness of moose was variable and not indicative of a pathway effect. Notably, moose prompted numerous and large gatherings of wildlife watchers, particularly where the TPR crossed the Snake River in Moose, Wyoming. A large number of our off-road and off-pathway observations were attributed to visitors venturing down along the river to see moose in this area. Even with off-road and off-path activities and direct approaches by people, moose opted to stay, sometimes for weeks, near the TPR in the treatment, offering visitors moose viewing opportunities from the road. Thus, moose did not appear to be notably disturbed or displaced by human activities in the treatment, including pathway activities in particular.

Wildlife responses to human activities are complex, but previous history of an animal's exposure to human activity plays an important role in understanding current responses to potential disturbances (Bejder et al. 2006, Stankowich 2008, Bejder et al. 2009). In park settings, or in areas where hunting is prohibited and people do not approach wildlife directly, animals that are exposed to high-use human activity areas such as park roads have shown lower levels of responsiveness to human activities than might be expected (Thompson and Henderson 1998, Burson et al. 2000, Papouchis et al. 2001, Borkowski et al. 2006). The Teton Park Road has afforded access and wildlife viewing opportunities to millions of park visitors for decades. Prior to pathway construction in 2008, ungulates were visible from the road, and many visitors stopped on the road to view elk and pronghorn, in particular. Assuming a majority of the ungulates observed in the study area were habitual summer residents that annually returned to these habitats, as was demonstrated for elk via GPS-collar movement data during the study (Sawyer et al. 2011), these animals would have been familiar with relatively predictable and common human activities that occur in the park's transportation corridor. Frequent exposure to predictable activities that result in neutral outcomes can induce habituation, a waning of response to inconsequential stimulus (Eibl-Eibesfeldt 1970). This learned response is a behavioral adaptation that allows animals to dedicate attention and energy toward fitness-enhancing behaviors such as feeding, grooming, resting and mating rather than expending energy to flee non-threatening activities (Thompson and Henderson 1998). Ungulates have been known to habituate to regular exposure of non-lethal human activities (Stankowich 2008). Elk in particular have shown habituation patterns along roads and other areas disturbed by human activities (Lyon and Ward 1982, Morrison et al. 1995, Thompson and Henderson 1998).

Ungulates that occupied habitat visible from park roads may not be representative of the entire population of ungulates in the larger region. There is potentially a self-segregating contingent of ungulates from the larger population that were less tolerant of human activities and actively avoided habitats seen from park roads even prior to the onset of this study (Bejder et al. 2006, Vistnes and Nellemann 2007). Nevertheless, for ungulates that do not avoid roads, such as those observed in our study, lack of displacement from human disturbance and reduced behavioral responsiveness of individual animals can have negative impacts on fitness and population persistence. For example, animals that do not exhibit strong behavioral avoidance of humans may still suffer fitness impacts if the human disturbance is substantial but the costs of moving to avoid it are overly high (George and Crooks 2006). Decreased behavioral responsiveness in ungulates may also reduce their ability to visually detect predators and other potential threats (Brown et al. In review.). Moreover, although tolerance to human activities may provide opportunities for park visitors to view ungulates from the road, it may also lead to increased human conflict such as negative encounters with recreationists (Olliff and Caslick 2003) or collisions with vehicles (Ament et al. 2008), major concerns for park managers. Long-term studies would be necessary to evaluate the actual demographic impacts of pathway activity on ungulate populations, within and beyond habitats that can be seen from the road.

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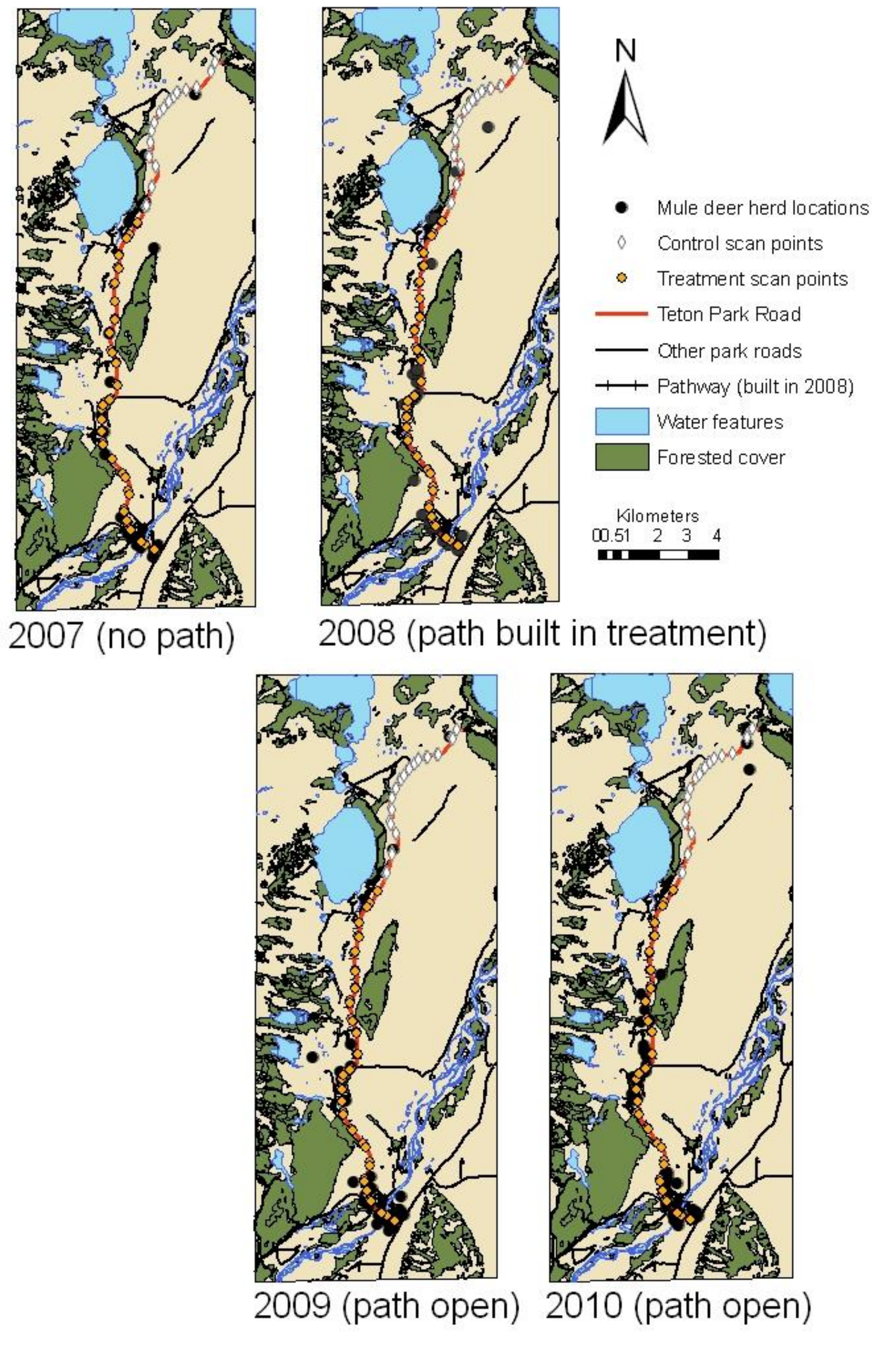
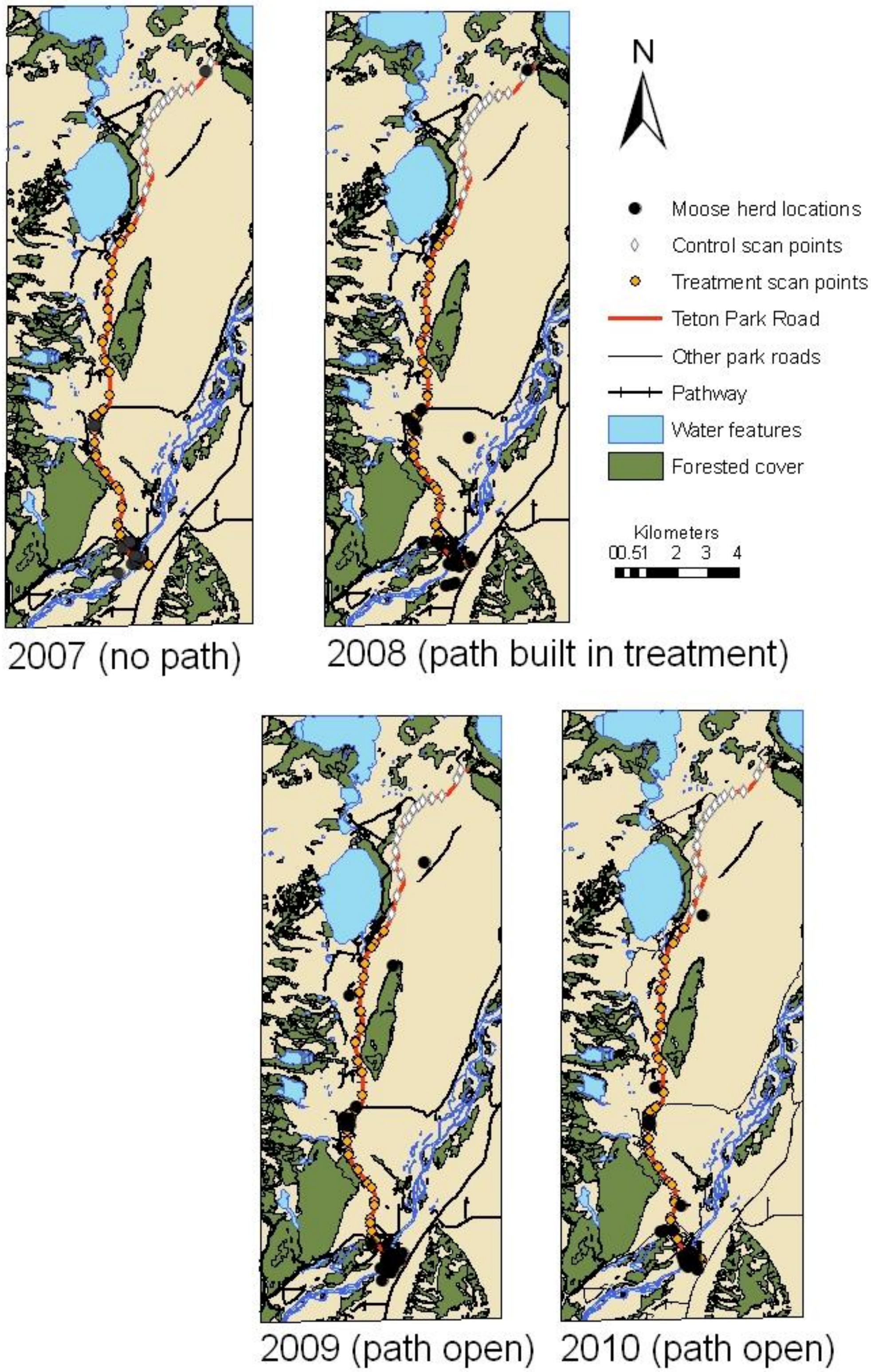
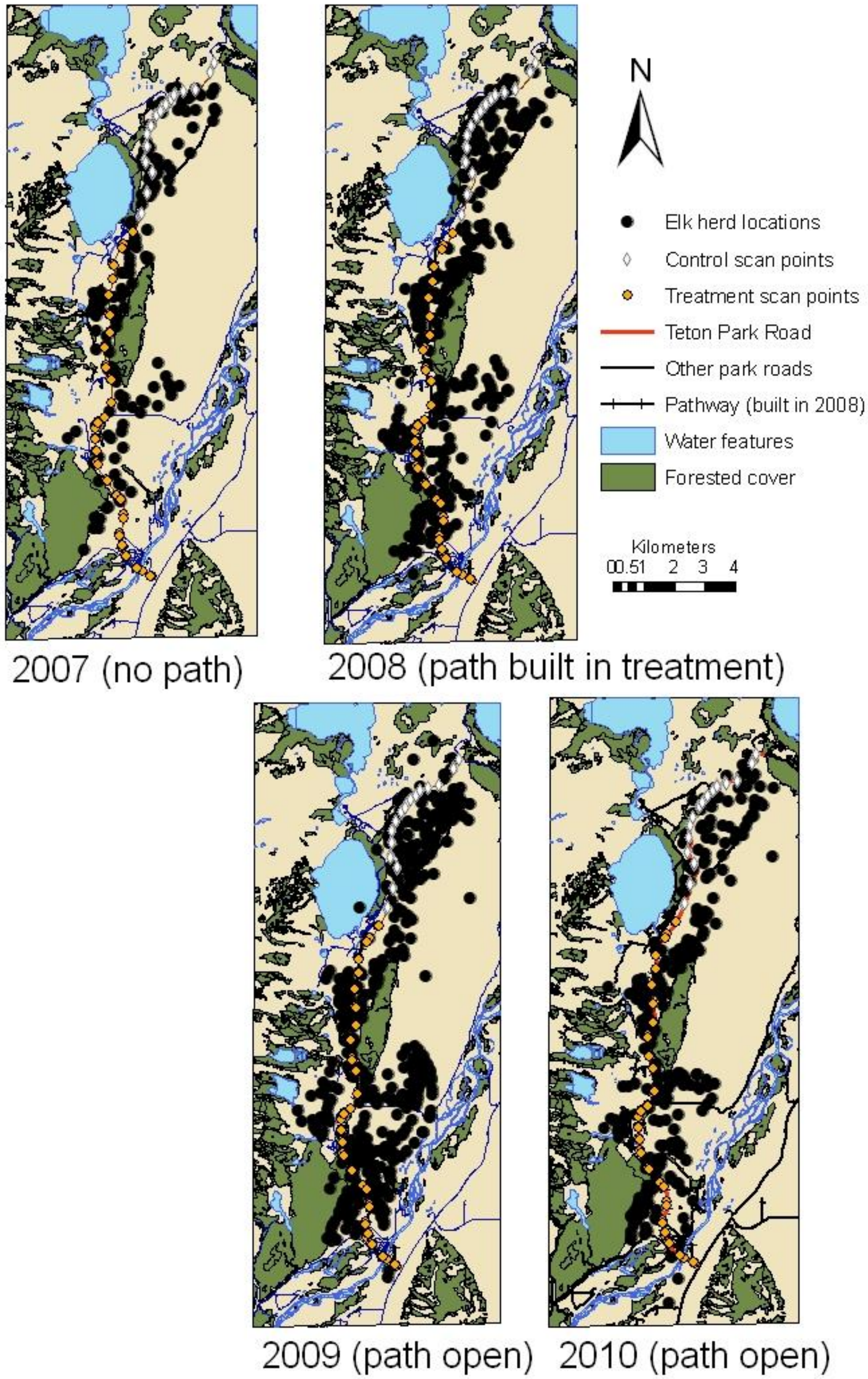


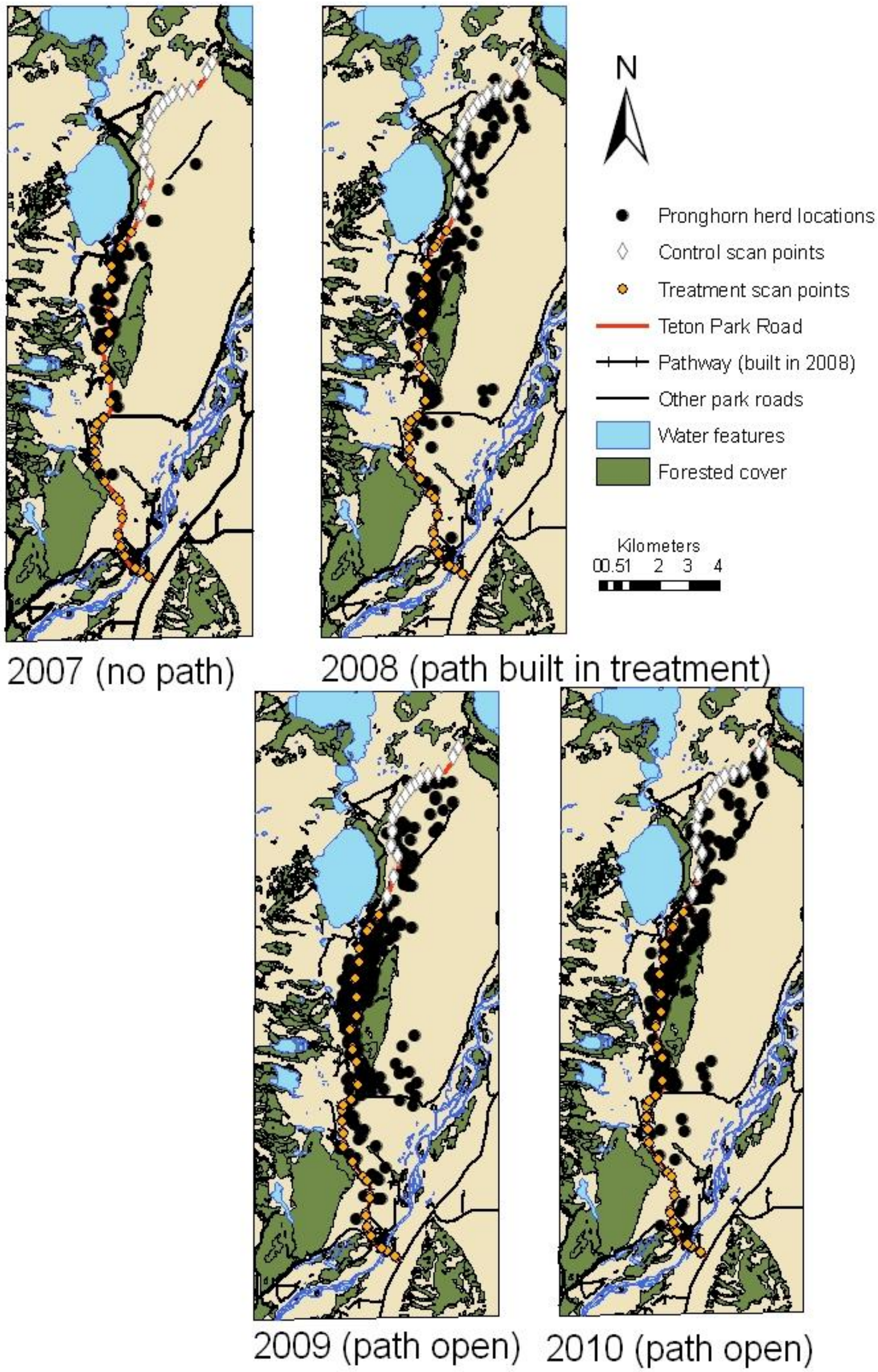
Appendix Map 1. Locations of mule deer groups observed from Teton Park Road between Moose and Spalding Bay Road during road surveys conducted between June and October 2007-2010 in Grand Teton National Park.



Appendix Map 2. Locations of moose groups observed from Teton Park Road between Moose and Spalding Bay Road during road surveys conducted between June and October 2007-2010 in Grand Teton National Park.



Appendix Map 3. Locations of elk groups observed from Teton Park Road between Moose and Spalding Bay Road during road surveys conducted between June and October 2007-2010 in Grand Teton National Park.



Appendix Map 4. Locations of pronghorn antelope groups observed from Teton Park Road between Moose and Spalding Bay Road during road surveys conducted between June and October 2007-2010 in Grand Teton National Park.